

THE MORPHOLOGICAL AND ANATOMICAL INTERPRETATION AND
IDENTIFICATION OF CHARRED VEGETATIVE
PARENCHYMATOUS PLANT REMAINS

by

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"Each individual Gar fish (Lepisosteus spp.) could contribute literally hundreds of bones and scales that can be identified to the generic level. On the other hand, there is rarely anything left of a potato."

Wing and Brown (1979, p.8) on the preservation and identification of archaeological remains.

ABSTRACT

This research project has attempted to develop a methodology for the identification of charred remains of useful non-woody vegetative parts of plants by the use of morphological and anatomical characters. A large number of taxa have been observed covering a wide morphological, anatomical, ethnographic and taxonomic range. The chosen taxa cover a geographic area from Western Europe, through the Mediterranean to the Near East.

Anatomy of fresh material viewed under the light microscope has been used to interpret the anatomy of experimentally charred tissues viewed under the Scanning Electron Microscope. Classical morphological and anatomical characters have been used as well as artifactual characters caused by charring.

Literature covering root and tuber domestication and the exploitation of roots and tubers as wild resources are reviewed. The origins of root crops in Europe and the Near East is discussed and compared with the origin of root and tuber crops in the tropics. The application of morphological terms such as rhizome, rootstock and corm as well as the use of anatomical and morphological characters

of the tissues under observation for classification and identification are discussed.

The results first describe the characters of charred non-woody vegetative tissue, so that in the separate descriptions of the charcoal each taxon that follows the morphology and anatomy may be interpreted. Those characters that are diagnosed are indicated. Archaeological charcoal that has been analysed is also described.

The results are discussed with a view to methods of identification of parenchymatous tissues and a manual dichotomous key is presented. Applications of the research are examined. Finally a list of concluding points is put forward.

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CHAPTER ONE - INTRODUCTION

1.1 THE IDENTIFICATION OF VEGETATIVE PARENCHYMATOUS PLANT REMAINS

The remains of vegetative parenchymatous organs, roots, tubers rhizomes, corms etc. are rarely identified from the charred plant remains recovered from archaeological sites. This is despite the often frequent occurrence of such tissues in archaeological samples. Methods for their identification have not been developed and it is only the relatively few remains, where preservation of the external morphology is good, that have been positively identified.

Any inference drawn from the plant remains recovered from archaeological sites is based on the classes of plant remains that are, at present possible to identify. These are most commonly seeds, the hard parts of some fruits, cereal remains, wood and pollen. If samples contain a high proportion of charred remains that are unidentifiable, using the present methods of identification, any inference drawn from those remains that are identified will be biased. Unless methods of identification are available for vegetative parenchymatous tissues it is understandable, if at the level of sorting,

such remains are categorised with what really are unidentifiable fragments of charred tissue.

The broad aims of this research are to recognise diagnostic characters in charred vegetative parenchymatous tissues with a view to the development of methods of identification for remains recovered from archaeological sites. Specific aims and objectives are examined in section 1.2.

Identifications of the archaeological remains of vegetative parenchymatous organs are few. Of these remains most are dessicated, a considerably small number being of charred tissues. Towle (1961), identified remains of both Manihot esculenta Crantz and Canna edulis Ker. These early identifications were followed by those of Patterson and Mosely (1968) of Canna edulis and those of Cohen (1975, 1978) of both Canna edulis and Manihot esculenta. More recently Ugent et al have identified Solanum tuberosum L. (1981, 1987), Ipomoea batatas (L.) Lam (1981), Canna edulis (1984) and Manihot esculenta (1985). These remains, all South American, were all preserved by desiccation rather than charring. All the remains identified by Ugent et al with the exception of the second Solanum tuberosum (1987) were from the exceptionally rich Casma Valley site in Peru.

Identified charred remains are far fewer. Rosendhal and Yen (1971) identified charred Ipomoea batatas remains and Martins (1976) the remains of Ipomoea batatas, Solanum tuberosum, Manihot esculenta, Ullucus tuberosus Caldas, Tropaeolum tuberosum Ruiz and Pav. and Xanthosoma Schott. The work of Martins is extremely important in that it marks perhaps the first use of anatomical criteria, examined by Scanning Electron microscopy, in the identification of vegetative parenchymatous tissues. Though this work takes a justified archaeological viewpoint in that the development of criteria for identification of the plant remains is secondary to the discussion of the inferences drawn from them, the work remains outstanding in its contribution to the study of these archaeological plant remains. Vegetative parenchymatous remains recovered from Britain and Northern Europe identified using morphological criteria include those of Arrhenatherum elatius ssp. bulbosum by Allison and Godwin (1948), Parrington (1978) and Heslop (1987); Conopodium majus by Moffet (L. Moffet pers comm) and Ranunculus ficaria by Bakels (1988).

The work of Standifer (1987) is important in that it emphasises the need for examining modern vegetative parenchymatous tissues in developing methods of identifying archaeological remains. Much of the

archaeological material examined by Martins however, illustrates the necessity for the effects of taphonomy to be recognised. This is an aspect of experimental archaeological identification that work, such as that of Standifer, rarely takes into account.

1.2 AIMS AND OBJECTIVES

The broad aims of this research have already been outlined. Before the taxa to be examined in this research may be determined specific aims and objectives have to be decided. Taxa may then be selected to reflect the aims rather than allowing taxa to determine the aims by their availability. Nevertheless, availability still determines the ultimate selection of taxa, though the research aims remain fundamentally unaltered.

Assuming that the number of taxa that could potentially form vegetative parenchymatous archaeological remains are too great to allow an exhaustive and thorough investigation covering a wide area a limited number of taxa had to be selected to satisfy either of two requirements.

- 1) To provide criteria to identify the potential remains of a limited group of taxa whether the group was restricted

geographically, taxonomically, morphologically or ethnographically. This would develop an exhaustive though limited methodology for the identification of taxa, linked in some way or other.

- 2) To provide criteria to identify taxa covering a range geographically, taxonomically, morphologically and ethnobotanically. The examination would not be exhaustive in any one of these areas though would it give a much broader spectrum of data concerning vegetative parenchymatous remains.

In the short term it is more profitable to concentrate upon the examination of limited groups of taxa. This would allow the development of criteria which would enable the identification of vegetative parenchymatous remains pertaining to specific archaeological questions or particular archaeological sites. The archaeological implications of such an examination would be more immediate than the second contrasting type of study. This would allow the development of criteria enabling the identification of a very wide range of taxa covering varied morphological types and ethnobotanical uses from a wide geographical area. Such a course of study would

allow immediate application to few particular archaeological questions or archaeological sites though it would provide data relevant to the identification of vegetative parenchymatous plant remains on a much larger scale.

Considering the lack of published work concerning the identification of vegetative parenchymatous tissues, whether charred or preserved by other methods, and the limited relevance to archaeobotany in general of a research programme restricted either taxonomically, geographically, morphologically or ethnobotanically, a course of study reflecting a relatively wide range of variables was chosen. The taxonomic, ethnobotanical and morphological range selected was as wide as the availability of taxa would allow. It is only geographically that restrictions and limitations were made.

It was initially decided to restrict taxa to those occurring in Britain, Western Europe, the Mediterranean region and the Near East. While this was adhered to in the majority of cases, exceptions were made on two accounts. Firstly species indigenous to these areas that were not available were substituted for by closely related taxa whose vegetative organs were understood to be similar

in all respects as well as having similar ethnobotanical uses. Secondly, species were included that were not indigenous to these areas but were possibly imported into them and therefore likely to occur archaeologically. It was decided to examine both cultivated and wild taxa, though the latter form the majority, rather than to restrict any application to non-agrarian sites.

General taphonomic, ethnographic, morphological and anatomical considerations will be examined with reference to the relevant literature prior to the description of the materials and methods employed in the research. The results and a full discussion of the research follow this. With the exception of the discussion, chapters are to a large extent independent of each other dealing with different aspects of the research and the results. The results and discussion are illustrated by a series of seventy plates each with ten figures contained in the second volume of this thesis.

CHAPTER TWO - TAPHONOMY, DOMESTICATION AND ETHNOBOTANY OF VEGETATIVE PARENCHYMATOUS ORGANS

2.1 INTRODUCTION

In this chapter certain areas relevant to this research that do not have a directly anatomical or morphological aspect will be examined. The subjects of taphonomy, domestication and ethnobotany will all be reviewed with reference to the relevant literature.

There are several different classes of literature from which data relevant to aspects of ethnobotany may be drawn. Herbal and medical books such as Gerrard (1633) and Culpepper (1669) and the more modern Redwood et al (1885) and Potter (1950): dictionaries of economic plants such as Johnson (1862), Hendrick (1919) and Tanaka (1976): numerous ethnobotanical studies such as those by Smith (1923, 1932), Morton (1963), Erichsen-Brown (1979), Turner (1981), Turner and Kuhnlein (1982) and Felger and Moser (1985) on North American plant utilization, Bailey and Danin (1981) on plant use in Sinai and the Negev, and that of Lawrence (1968) on the Aboriginal peoples of Australia: floras such as Tackholm and Drar (1950) and Guest et al (1966); and finally the more generalised and theoretical studies, such as that of Harris (1977) that draw upon a

wide range of ethnographic examples.

The literature drawn upon here, relevant to the subjects of cultivation and domestication of 'root and tuber' plants included both monographs on species with particular reference to their domestication and the more wide ranging reviews of the origins of agriculture drawing upon many different examples.

Archaeological evidence for patterns of exploitation of wild 'root and tuber' foods, and their eventual domestication is presently rare due to the problems encountered in the identification of vegetative parenchymatous remains - hence the present research. There is however a particularly large body of information to be gained from the interpretation of such remains and their importance must not be underestimated.

In this chapter, processes which influence the taphonomy of plant products ranging from harvesting and processing of fleshy vegetative organs to their preservation and burial, are examined with a view to the types of plant remains likely to be encountered in archaeological deposits. Following this, the adoption of cultivation and eventual domestication of vegetative parenchymatous organs is reviewed with reference to certain taxa under study

here and their role in agricultural origins. Ethnographic data and their sources for each of the wild taxa under examination is then given.

2.2 TAPHONOMIC PROCESSES

2.2.1 Introduction

The taphonomic process in terms of plant remains, in its widest sense, may be taken to include all stages between the removal of plants, or parts of plants, from where they grow, through preservation in the archaeological record to a point directly prior to excavation by the archaeologist. The whole taphonomic process may be divided into five stages (Hillman, pers. comm.):-

- i) Off-site harvesting and processing and arrival on site
- ii) On-site processing
- iii) Preservation
- iv) Post-preservation dispersal and deposition
- v) Post-deposition factors

The presence and state of plant tissues on an archaeological site prior to excavation is affected by processes at all these stages. While close analogies may be drawn between the types of plant tissues under study here and from other plant remains and their different

modes of preservation, it is necessary to examine closely the taphonomic processes affecting charred remains of vegetative parenchymatous tissues alone since significant differences do occur.

In relation to the plant tissues under study here, the third stage in the taphonomic process, preservation - in this case charring - is the most important factor to affect the remains. Processes prior to this affect which plant parts become charred and how. Processes subsequent to preservation determine the survival of the charcoal fragments prior to excavation. The effects of charring as a mode of preservation on vegetative parenchymatous tissues forms the present research. The pre-charring and post-charring factors affecting these particular plant remains will be dealt with below.

2.2.2 Pre-charring Taphonomic Processes - Off Site Processes

The process of harvesting vegetative parenchymatous organs depends very much on the nature of the particular plant being harvested. It is possible to harvest many of these types of plants simply by pulling on the aerial parts. This is often easily achieved with many rootstock and rhizomatous plants, many of which have the storage organ

close to substrate surface. Many roots, plants with a tuberous morphology and plants whose aerial parts die back completely in autumn and winter, the most likely time of harvesting, have to be harvested by digging either by hand or with the aid of digging implements. This is demonstrated by O'Connell et al (1983) discussing harvesting methods used by the Alyawara speaking Australian aborigines. Cyperus rotundus having a shallow rooting rhizomatous system may be dug by hand whereas the deeper lying roots have to be dug using wooden or metal digging sticks. Donkin (1970) discusses the use of digging sticks as a basic agricultural implement ranging from being no more than a pointed stick, possibly fire hardened at one end, to a metal or stone tipped stick, some of which may be weighted.

Many of the taxa under study here are wild foods which, in recent times, have been harvested as an occasional resource either as a luxury or a famine food. While some may have served as staple resources the majority will not be affected by factors such as intentional off site storage and propagation.

The practice of leaving parts of vegetative parenchymatous organs in the ground, taking only what is needed facilitates both storage and propagation (Harris 1977).

Many Dioscorea species are ideally suited to this and the practice is common throughout the tropics and sub-tropics. However the nature of many of the plants under examination here does not allow easy vegetative propagation. The practice would be seasonally limited by the biennial nature of many of the plants and the seasonal nature of the storage organs of the more perennial plants in temperate regions.

It has been established that the plants with vegetative storage organs in the Northern temperate regions, are harvested in their entirety, rather than, for reasons of storage or propagation, harvested partially. With the whole plant harvested off-site two options are available- to take the whole plant back to the site for processing or to partially process the plant off-site. Several factors are at play here. If, for example, a rhizome with large leafy aerial parts, such as a Typha species, is harvested and the aerial parts are not required for thatching, basketwork etc., then it is likely that the leaves would be removed off-site. This would facilitate ease of carry through both weight and volume loss. Turner and Kuhnlein (1982) state how the 'tops' of an edible rhizome of Trifolium wormskioidii and the root of Potentilla anserina ssp. pacifica are removed off-site by Indians of the North West American coast. However, the

same plant may have fibrous roots emerging from the rhizome. It is unlikely that these would be removed off-site since their removal would make little difference to weight or volume but would be rather time consuming. This is important in determining which plant parts arrive on-site.

2.2.3 Pre-charring Taphonomic Processes - On Site Processes

While off-site processing determines which plant materials enter the site and which will never be found on site, on-site processing determines whether preservation of those plant materials in the archaeological record takes place. In this sense, on-site processing is of greater importance to taphonomy and is considered by many to be the starting point of the taphonomic process. However when examining the fate of 'root and tuber' resources, off-site processing is of considerable importance, and must not be underestimated.

The transformation of partially processed or non-processed 'root and tuber' plant materials into a product that may be used either as food or medicinally ranges from the very simple to the very complex. Different processes will of course be employed for different tissue types and

different taxa, though there may be more than one method used to process the same tissue of a single species. The cooking of the corm of Colocasia esculenta in Papua New Guinea is such an example. Here the tissue of the corm may be boiled, roasted or par-boiled followed by frying (Harris pers. comm.)

O'Connel et al (1982) describe the simple scraping of tubers such as Cyperus esculentus to remove dirt and grit. This would be followed by roasting prior to pounding to separate the flesh from fibres. Plowman (1967) describes the processing of many New World Aroids, including roasting, boiling, baking, frying, steaming, grating, pulverising for the extraction of starch and the production of 'poi' a fermented paste made from the crushed corms of Colocasia esculenta. In Brazil the crushed cooked corm of this species is mixed with oatmeal and made into a type of bread.

Morton (1975) describes the processing of Typha rhizomes. These are cooked by roasting or boiling after the outer spongy (aerenchymatous) cortex has been stripped off. Alternately the rhizomes may be stripped, then ground and separated from any fibre by dry sieving or water flotation.

Cooking by steaming is a common method employed for the processing of 'roots and tubers'. Both Norton (1981) and Turner and Kuhnlein (1982) describe the use of steaming pits, kettles, boxes and mounds. Here hot rocks are piled with alternate layers of the edible roots and damp vegetation. Water is then poured over the rocks and the pit or pile covered with sand allowing the build up of steam, cooking the roots. Turner and Kuhnlein (1982) note that this is a very skilled operation and may easily result in burning if too many hot rocks or too little water is used.

The medicinal use of 'roots and tubers' often involves pulverisation followed by mixing with water or animal fat for the use as salves or washes for colds and chest infections. O'Connell et al (1983) and Bailey and Danin (1981) describe the peeling of the root of Cynomorium coccineum L. which is then either eaten raw or ground and boiled with water to produce a drink. Further, the root of Convolvulus hystrix Vahl must be dug up under starlight, ground, boiled in water and drunk or strained and added to goats milk to produce a drink.

Detoxification is an important technique in the processing of many 'root and tuber' resources. Hydrocyanic acid, the active poison in Manihot esculenta (Manioc) is removed by

different methods depending on whether sweet or bitter manioc is involved. Within the taxonomically complex group of cultivated Manihot esculenta there is a range from one extreme where the HCN is restricted to the phelloderm (sweet) to where the HCN is distributed throughout all the tissues of the tuber (bitter). Detoxification of sweet manioc is achieved by the boiling and roasting of the whole tubers followed by the peeling of the outer tissues containing the HCN. Bitter manioc detoxification is more complicated due to the nature of the distribution of the HCN throughout the tuber. The tubers are peeled and then grated to produce a pulp. This is then squeezed in basket-work cylinders to extract the HCN. The pulp is then heated over a fire to produce a type of meal or bread (Renvoize 1970, Harris 1972).

The operations involved in detoxification often lead to the reduction of amyliiferous parenchymatous tissues to a coarse or fine flour. The production of bread from 'root and tuber' flour is not uncommon whether the flour is a product of detoxification or not. Johnson (1862) remarks on the production of bread from the root flour of Polygonum bistorta in Russia and Siberia and even from the root of Pastinaca sativa where it was either employed alone or mixed with cereal flour.

On-site processing of plant materials may potentially result in several classes of plant remains. Firstly there are the final products of processing intended for use either as food or medicine. This may become charred at any time during the processing of the plant material and not necessarily at the end. Secondly, throughout all the stages of processing waste products will be created as a direct result of the processing method. These include remains such as peeled epidermis or periderm, fibre and vascular tracts, 'woody regions' of roots etc. All are plant fragments specifically intended as waste products and potentially identifiable as resulting from specific stages in processing. Thirdly there will be the whole or fragmented unprocessed plant organs. These may include damaged or fungally infested tissues. The life of parenchymatous organs once dug is short compared with that of grain and so unless careful post-harvesting storage is undertaken the likelihood of tissues becoming infested with fungi or bacteria would not be uncommon. Accidental charring and unwanted edible organs that are thrown away may also occur.

2.2.4 Preservation

The actual effects of charring on the morphology and anatomy of vegetative parenchymatous tissues derived from

roots, tubers, rhizomes etc. forms the basis of the research presented here. The nature of domestic fires in which such tissues are likely to get charred are examined in chapter four with a view to the experimental method employed here. Once the plant tissues have become charred, (reduced, though usually only partially, to elemental carbon), then post-preservation factors are in operation.

2.2.5 Post-preservation Factors

Factors affecting charred plant tissues after preservation by their exposure to fire may be divided firstly into those of dispersal and deposition and secondly the effects of the depositional environment. Both may affect the survival of charred remains prior to excavation.

Factors related to the dispersal and deposition of plant remains are restricted to charred plant tissues since with both dessicated and waterlogged remains preservation actually occurs in the depositional environment. Charred remains may be deposited in situ in the environment in which they were charred, often a domestic fire, or they may be dispersed from this and be deposited elsewhere on site. The process of dispersal may bring about mechanical damage to the fragments of charred tissue possibly

resulting in partial or complete disintegration.

Once in the environment of deposition both direct and indirect mechanical damage may be caused. Factors affecting the extent to which this occurs have been defined by Hillman (1981):-

- 1) The period of post-depositional exposure prior to protection from overlying deposits.
- 2) The degree of protection derived from overlying deposits.
- 3) The period of burial - charred remains deteriorate with age even under optimal conditions.

The post-depositional environment will have an effect upon any charred remains up to a point directly prior to excavation by the archaeologist. The post-excavation history of charred remains - recovery, sorting etc. are not part of the taphonomic process.

2.3 CULTIVATION AND DOMESTICATION

2.3.1 Introduction

The majority of taxa under study in this research are gathered from the wild rather than cultivated. A few of the taxa however are cultivated, and the specimens chosen

had been grown under modern extensive agricultural methods. The taxa are all typical of Northern temperate European and Near Eastern fleshy 'tap root' crops. The significance of this will be discussed below. In this section aspects of 'root and tuber' domestication will be reviewed with special reference to the Northern temperate root crops. The origins of tropical 'root and tuber' agriculture will be briefly examined. Specific use of the terms 'domestication' and 'cultivation' will be examined with a view to their application to the taxa under study here as well as 'root and tuber' crops in general. Finally each of the 'non-wild' taxa under study will be dealt with separately, their origin use and history being outlined.

2.3.2 The origins of 'Root and Tuber' agriculture

Hawkes (1986) states that once both planting and harvesting occur as seasonal operations, then 'agriculture' could then be said to have begun. In examining the origin of this process for 'root and tuber' crops the questions of both 'where' and 'how' may be addressed.

'Root and tuber' agriculture is most highly developed in the tropical areas of Asia, Africa and the Americas

(Harris 1969). However, as is pointed out by both Sauer (1952) and Harris (1972), the ancestors of the major tuber crops most likely developed in areas with marked dry seasons, the development of tubers being naturally selected for perennation and storage to survive periods of drought. Therefore, rather than search for the origin of these crops in tropical rain forests attention should be turned towards 'summer-green rain forest or scrub regions with a well marked dry season' (Hawkes 1986). Once domesticated, and once associated agricultural practices had been developed these crops were taken into the tropical regions with which they are now associated.

Sauer (1950) and, more recently, Hawkes (1986) have indicated the existence of two other distinct classes of tuber crop cultivation found almost solely in South America. The origins for neither may be accounted for by the theories relating to the origins of tropical vegiculture. These are firstly the species associated with the medium altitude warmer valleys of the Andes and elsewhere, and secondly the high altitude cold resistant species also of the Andes. Far more evidence from many sources is needed before the origins of these crops is understood.

The processes of 'root and tuber' cultivation is poorly understood and though many theories have been put forward,

there remains a substantial lack of evidence to support them. Theories relating to the origins of 'root and tuber' cultivation rely heavily on the fact of vegetative reproduction. Vegeculture is dependant on this in a similar way to seed culture being dependant on sexual reproduction.

Manglesdorf et al. (1971) quote Payne (1892) as suggesting that agriculture as a whole originated with root crop culture since soil disturbance of the sort that would have resulted from the digging of roots is a character of tillage. The practices of digging up roots and planting are very similar and the processes of root consumption are very simple. Sauer (1959) postulates similar arguments. Pre-agrarian people had spare time in which to look for and dig up roots to improve their diet, although Manglesdorf et al. state rightly that evidence for this is lacking.

Hawkes (1969) reviews the theory that states that 'root and tuber' cultivation came prior to that of seeds since the processes of cultivation - planting and cultivation-are similar for all roots and tubers. For seed and fruit crops the cultivation processes are all very varied. Again there is no evidence to support this. Further, Hawkes states that both seed and 'root and tuber'

cultivation originated in areas where the plants were available and most amenable to cultivation. For 'roots and tubers' this was in the tropics.

Wherever 'root and tuber' cultivation took place the processes between simple collection and actual cultivation almost certainly varied. Sauer (1952) suggests that the digging of tubers gives an incomplete harvest, the remaining tuber parts giving rise to a new crop the following year. These eventually became perennial digging plots. It is a short step between this occurring in the ignorance of the human collector and the active process of planting or leaving tuber parts in the dug hole. This has been mentioned by McConnel (1957) and Specht (1958) as cited by Harris (1977).

Sauer (1952) and Hawkes (1969) also developed a theory that waste fragments of collected wild tuber resources discarded close to early habitation sites, were able to vegetatively propagate ultimately leading to their harvesting and deliberate planting.

Discussion of various theories relating to the origins of 'root and tuber' agriculture could be expanded almost limitlessly. Nevertheless the ground has been sufficiently covered to allow a comparative examination

of the role of cultivated and domesticated root and tuber crops in Northern temperate agriculture of Europe and the Near East. First however, it is necessary to consider the terms domestication and cultivation with specific reference to the taxa under examination here.

2.3.3 Domestication

Hawkes (1976) outlines a succession of activities leading from the collection of wild plants to their cultivation and ultimately to their domestication. Any definition of the final stage, domestication, has to take into account the previous stages in the succession and possibility that long periods of cultivation may not necessarily culminate in domestication.

Both Hillman (1978) and Simmonds (1979) have defined 'domestication' in the strict narrow sense adopted by many authors. A much broader definition is proposed by Rindos (1980, 1984) but it is too broad to be of any value in the present discussion. Both Hillman and Simmonds state that domestication in the narrow sense involves an alteration of the genetic structure allowing plants to become more suited to conditions provided by human societies rather than those of their natural environment. Human selection therefore substitutes for natural selection. If

domestication involves a genetic change, whether at the level of the individual or the population, the domesticate will not be able to revert back to the wild state. This often means that it will die if not grown under conditions of human cultivation. Where cultivation of a population induces physiological or morphological changes that can still revert to the wild state then domestication in the strict sense cannot be said to have occurred. For example Pastinaca sativa is an extremely variable cultivated 'wild' species. It is completely fertile when crossed with truly wild members of the same species and will revert back to the wild type unless prevented from outbreeding (Smith 1976). Pastinaca sativa has undergone a high level of cultivation but is not domesticated.

Simmons (1979) states that domestication is a culmination of a long period of association with people and only after this exploitation could be said to be truly domesticated. However one only needs to look at the parsnip to see that the process beginning with the collection and gathering of wild foods and leading on to their eventual cultivation need not culminate in their domestication. Where genetic change is required to effect stability in a cultivated plant with desired traits, then domestication is likely to take place. If the desired traits already exist within

the range of phenotypic plasticity in one genotype then domestication will not necessarily take place.

Domestication in the strict sense, in which genetic change has taken place, may be observed in root crops such as Beta vulgaris ssp. vulgaris and Daucus carota ssp. sativus. The genetic change is reflected in the taxonomic status of the domesticates as being distinct from the 'wild' relatives, the role of the root and tuber resources in the origins of agriculture in temperate areas will be considered.

2.3.4 'Root and Tubers' as Staples

A striking feature of the established 'root and tuber' crops of the world is their ability to reproduce vegetatively. This is mostly achieved by the swollen organs being derived from stem tissue and therefore containing nodes either along their length or at their distal or proximal ends. Examples of these being the yams (Dioscorea species) and Taro (Colocasia esculenta). Notable exceptions are Manioc (Manihot esculenta) a root tuber reproduced vegetatively from stem cuttings and the sweet potato (Ipomoea batatas) reproduced by adventitious shoots produced directly from the root tissues of its tuber.

The established root crops of the Northern hemisphere are mostly biennial, swollen and fleshy, secondary structures developed for one winter's perennation prior to flowering, setting of seed, and finally death of the plant. These are composed of non-perennial root tissue and lack the ability to multiply vegetatively by any method.

The attributes of the types of plants that give rise to vegiculture are long term perennation and vegetative propagation; these are not possessed by the now established root crops indigenous to the Northern temperate regions of Europe and the Near East.

Harris (1969) states that vegiculture is dependent on vegetative reproduction and seed culture dependent on sexual reproduction. The cultivated and domesticated northern temperate roots under study here are still dependant on sexual reproduction and are, despite being root crops, still part of seed culture and not vegiculture.

Leading on from this it can be seen that, unlike the tropical vegetatively reproducing 'root and tuber' crops, the Northern temperate root crops were unlikely to have been responsible for the origins of agriculture in this area, or even a part of early agriculture. Rather, they

were more likely to have remained as wild resources until the seed culture based agricultural system became established and developed technically to an extent that would allow their incorporation - if only on a very small scale.

The main disadvantage of these crops is the inability of the part of the plant used as food to also be used in propagation. The plants are still dependant on seed for reproduction. This may have contributed to their failure to be utilised as important sources of carbohydrate. Their principle role as with many wild resources was to provide variety or as an emergency food when established food sources failed, whether these were cultivated or wild. Their utilization as a staple is limited to very few cases.

Such root crops only became part of the regular diet when grown on a very small 'garden' scale or relatively recently when large extensive farming methods became common.

2.3.5 Origin and History of European and Near Eastern Cultivated Roots and Tubers

2.3.5.1 Introduction

It has been argued above that the cultivated, and in some cases also domesticated taxa, indigenous to Europe and the Near East were introduced into the agricultural system well after its establishment in the area. In many cases the selection of the more important desirable traits distinguishing cultivated varieties from their wild relatives has been comparatively recent. Characters such as de-ramification, fleshiness, non-woodiness and changes to the life cycle to suit human utilization, have been selected for in many cases. A brief history of the origin and possible domestication of the cultivated taxa under examination in the present research is given below. The taxa are Beta vulgaris ssp. vulgaris (Chenopodiaceae), Armoracia rusticana (Cruciferae), Brassica campestris ssp. rapifera (Cruciferae), Raphanus sativus var. radiculata (Cruciferae), Daucus carota ssp. sativus (Umbelliferae), Pastinaca sativus (Umbelliferae), Cichorium intybus (Compositae), Scorzonera hispanica (Compositae) and Cyperus esculentus (Cyperaceae). All apart from the last, which is a rhizome tuber, are fleshy secondary thickened dicotyledonous roots.

2.3.5.2 Species Considered

Beta vulgaris ssp. vulgaris

The forms of the leaf beets preceed the root beets and have been described by both early Greek and Roman writers. References to the root beets for both medicinal and culinary purposes have been given by Roman writers though no indication has been given that these were swollen rather than merely fleshy (Ford-Lloyd and Williams 1975). Simmonds (1976) suggests that Romans first used the root of Beta for animal food but it entered human diet in the third to fourth century AD. It did not enter the British diet until the fourteenth century AD. He also states that the red beet preceeded the sugar beet.

The taxonomic history of Beta suggested by Ford-Lloyd and Williams (1975) has an ancestral maritime beet B. vulgaris (sensu latu) giving rise to a number of sub-species. These are ssp. maritima, the present maritime beet with many varieties and ssp. pro-vulgaris giving rise to ssp. vulgaris, the root beets and ssp. cicla, the leaf beets.

Armoracia rusticana

Courter and Rhodes (1968) quote de Candolle (1886) as

concluding that the horse radish originated in the temperate regions of Eastern Europe. As one moved westwards through Europe the plant became rare and more scattered. Also according to de Candolle, the plant has been in cultivation for less than two thousand years because the plant is mentioned by Dioscorides in the first century AD but not in the earlier writings of Theophrastus (c372 to 287 BC). The horse radish is cultivated extensively under modern agricultural methods but the plants are both morphologically and anatomically similar to the wild plants. The plant is also sometimes grown in the higher altitudes in the tropics (Pursglove 1968).

Brassica campestris ssp. rapifera

Brassica campestris is a polymorphic group, classified into a number of sub-species, most of which are former Linnaean species, based upon complete inter-fertility (Olsson 1954). The sub-species oleifera is probably closest phylogenetically and morphologically to the wild type, sub-species eu-campestris, the former having both annual and biennial varieties. The wild type is an annual with a slender root. Sub-species rapifera, the true turnip, is biennial. Sub-species oleifera is thought to be the earliest cultivated form originating from

'campestris' weeds of older seed crops such as flax (Vavilov 1926), in pre-classical times. This gives rise to annual and biennial oil seed varieties. Two main centres of origin may be determined: firstly, the Mediterranean for European forms and secondly, Afghanistan and adjoining areas of Pakistan. Asia Minor, Transcaucasus and Iran may be considered secondary centres. The biennial variety in turn gives rise to subspecies rapifera, the true turnip, however its use in Europe and Britain by far preceeds that of the use of oil-seed. The latter was not cultivated in Europe until the thirteenth century whereas turnips were well known to the Romans. The modern turnip originated during the 'Great Turnip Era' in Europe between the 15th and 18th centuries.

Raphanus sativus var. radiculata

Three wild species of Raphanus exist, R. raphanistrum in Europe extending eastwards to the Volga and from the Mediterranean to the Caspian; R. maritimus (coastal) and R. landra (inland) extending from the Mediterranean to the Caspian and on the European coasts; R. rostratus extending from Greece to the Caspian. None may singly be considered as an ancestral form of the cultivated radish R. sativus. It is possible that all are responsible. The area of origin has been postulated as the Mediterranean to the

Caspian, though Werth (1937) has suggested a more easterly origin. Four varieties of the cultivated radish exist today, radiculata, niger, mougri and oleifera, all intercross freely with each other and with wild Raphanus species.

Early records of the niger variety exist on the internal walls of the pyramids dated at two thousand BC. This long white form of radish first appeared in Europe in the 16th century, the smaller globular forms not appearing until the 18th century. It is therefore considered that the niger type is ancestral to the much later radiculata variety. The area of origin is most probably east of the Mediterranean but the exact area is difficult to determine.

Daucus carota ssp. sativus

Daucus carota ssp. sativus, one of the many freely intercrossing sub-species of Daucus exists in Europe extending through to Afghanistan. In Britain it is generally woody though east of Europe it is very variable having a wide range of morphological characters. It varies in its degree of ramification, fleshiness and in colour, (Mackevic 1929). Afghanistan is the centre of diversity, early western carrots being derived from the

eastern anthocyanin carrot (ssp. carota). The yellow ssp. sativus, the Western carotene carrot, selected for its lack of anthocyanin which dyed food purple, superseded the purple carrot in the 17th and 18th centuries. Photoperiod changes have also played an important role in the evolution of the modern carrot (Banga 1957, Small 1977 and Brandenburg 1981).

Pastinaca sativa

The specimens under examination here are of the true wild type rather than of the cultivated and true fleshy type. The status of Pastinaca sativa as a cultivated species has already been discussed. The root has been cultivated since at least Greek times though the larger fleshy varieties known today are thought only to have been developed since the Middle Ages (Smith 1976).

Cichorium intybus

Though known to have been cultivated by the Romans the time and origin of the first cultivation is unknown. This is largely Mediterranean species but is first mentioned in herbals in the 16th century. It was introduced into cultivation in Britain in 1788 as a fodder crop but was largely unsuccessful (Grieves 1931). Cultivation of the

root crop is now important in the coffee industry.

Scorzonera hispanica

The cultivated root originated in Spain from wild S. hispanica populations and is now cultivated mainly in South to Southeast Europe. Early mentions of the root occur in Italian medical books of the 16th century though references to its use as a vegetable occur in France in 1660 and in Germany in 1770 (Körber-Grone 1986)

Cyperus esculentus

Cultivation of this taxon in Ancient Egypt was undoubtedly important though was probably restricted to the Nile Valley. Pre-dynastic remains of the tuber (Tackholm and Drar 1950), represent only local cultivation and it is difficult to say whether domestication has actually taken place though this has been claimed (Zohary and Hopf 1988).

2.3.6 Rhizome Cultivation and Domestication

2.3.6.1 Introduction

Considering the large number of rhizomes that form wild sources of carbohydrate it is remarkable that very few

have entered cultivation. Members of the Nymphaeaceae (Nuphar and Nymphaea) and Monocotyledonous families such as the Typhaceae (Typha), Cyperaceae (Scirpus, Schoenoplectus) and Butomaceae (Butomus) all provide valuable and important rhizomatous wild food resources. It is only the Zingiberaceae though, that have been cultivated for its rhizomes, important species being Zingiber officinale (Ginger), Curcuma domestica (Turmeric) and Alpinia galanga (Galanga). Few of the Zingiberaceous rhizomes may be considered as important sources of carbohydrate, rather than condiments or of medicinal use. The history of the cultivation of these species will be outlined below.

The cultivated Zingiberaceous species are propagated by small portions of the rhizome containing one or two buds. These are known as setts. A good tilth is required for planting since hard ground produces deformed rhizomes. Setts may also be planted in ridges to facilitate harvesting. Curcuma domestica and Zingiber officinale take nine to ten months to grow before harvesting although Curcuma zedoaria takes a full two years for complete development. Crops are harvested by hand though mechanization is now beginning to take over.

The cultivation of these crops has considerable antiquity,

the rhizomes being planted between other crops such as yams or legumes (Pursglove 1972). Considering the success in cultivation of these species compared with the relatively few rhizomes in cultivation in general certain points could perhaps be mentioned. The Northern temperate rhizomes utilized as wild, especially as sources of starch, are often common species that could be harvested from the wild state without the specific need for cultivation. This is certainly true of Typha in certain localities. Also many of the wild rhizomes that are utilized grow in particular environments, such as the marshy conditions favoured by Typha which are not easy to replicate under the constraints imposed by cultivation. Having said this, crops such as rice are successfully cultivated under such conditions in many parts of the world. Generally though, with no particular pressure for rhizomes to be cultivated, domestication could not have taken place. These points, though important, are not specific to rhizomes and may apply to any morphological class of vegetative parenchymatous class of organ utilised as a wild food resource.

The specific lack of rhizomes in cultivation may be due to morphological rather than agronomic reasons. The horizontal 'spreading' organization of rhizomatous plants rather than the vertical central organization common to

other cultivated plants may create problems in cultivation. However similar problems do seem to have been solved in the cultivation of the Zingiberaceous species.

2.3.6.2 Species Considered

Alpinia galanga

Cultivated in Asia and Indonesia but imported by many areas of the world this rhizome is extensively used as a spice as well as having an important medicinal use. It was first imported into Europe in the Middle Ages (Pursglove 1972).

Curcuma domestica

As a source of the yellow food colouring, Turmeric, spice and cloth dye the rhizome of this species has been known to Indomalaysia for many centuries (Uphof 1968). It has also been important in cultivation in India. It is exported to many areas of the world.

Less well known and practically unexported species of Curcuma yield a starch used as a substitute for arrowroot. These are C. angustifolia Roxb. C. zedoaria (Berg.) Rosc.

(Pursglove 1972), and C. aeruginosa Roxb. (Uphof 1968).

Zingiber officinale

The rhizome of ginger has been used since 'ancient times' in many areas of Asia as a condiment for culinary purposes and use in certain beverages. Since then its use has spread throughout many parts of the world and is commercially grown in Jamaica, India, Hong Kong and Australia. Dried rhizomes, possibly peeled or scraped prior to drying are powdered for use. The rhizome is also used in local medicine in India and the Far East.

Zingiber officinale is unknown in the wild state; the country of origin of cultivation is also unknown. It was certainly present in India and China at an early date. Trade with China brought the spice to Europe in the ninth century and preserved ginger was imported into Europe as a sweetmeat in the Middle Ages (Pursglove 1972).

2.4 ETHNOGRAPHIC SOURCES

2.4.1 Introduction

Listed below are brief notes concerning the ethnographic sources relating to the use of each of the taxa under

study. This is not meant as an exhaustive examination of the ethnography of these plants and so works such as Uphofs 'Dictionary of Economic Plants' (1976) and Grieves 'Modern Herbal' (1931), neither of which cites primary sources, have been used extensively.

2.4.2 Species Considered

HYPOLEPIDACEAE

Pteridium aquilinum

The rhizome is said to have been eaten and cooked by the aboriginal peoples of Western Washington, North America (Norton 1979). Flour produced from the roasted and pounded rhizomes was made into a kind of bread. Further evidence is given by Morton (1963) and Rymer (1976) who state that bread was also made from bracken rhizomes by Maoris of New Zealand. Schery (1954) states that whole rhizomes were eaten by 'American Indians'.

ASPIDIACEAE

Dryopteris filix-mas

Turner and Kuhnlein (1982) state that the rootstocks of

this fern were eaten by Indians of the North West American Coast. The rootstocks would be boiled in stews with other similar ingredients such as the roots of Potentilla anserina ssp. pacifica, as well as berries, fish, fish eggs, grease and flour. Grieves (1931) remarks on a medicinal use for the rootstock, it having strong antithelmentic properties.

POLYPODIACEAE

Polypodium interjectum

Specific mention of this taxon has not been found though closely related species are known to be edible (Tanaka 1976).

NYMPHAEACEAE

Nuphar advena

Rhizomes of several species of Nuphar are eaten either raw, roasted or boiled. Uphof (1968) specifically mentions N. advena, an American species, Rogers (1980) N. luteum and Turner (1981) N. polysepalum. Rogers remarks on the practice of cutting up and drying the rhizomes for storage.

Nymphaea alba

Morton (1963) states that the rootstock (rhizome) of this taxon may be eaten either roasted or boiled. Uphof (1968) mentions N. alba rhizomes together with other Nymphaeae species as a source of starch recommended in times of emergency.

RANUNCULACEAE

Anemone nemorosa

The medicinal use of this species is documented by both Gerrard (1633) and by Culpepper (1669). The latter states that the chewed roots 'purgeth the head mightily'. Uphof (1968) mentions its use as a hyperamic and vesicans though should be used with care.

Ranunculus ficaria

Rogers (1980) states that all Ranunculus species are more or less poisonous though edible as an emergency food when cooked. The medicinal use of this species is remarked upon by both Johnson (1862) and Grieves (1931).

CARYOPHYLLACEAE

Gypsophila struthium

Together with other Gypsophila species this taxon is a source of Radix Saponariae Hispanicae, a cleansing and purging agent employed for skin diseases (Uphof 1968).

CHENOPODIACEAE

Beta vulgaris ssp. maritima

The root of the wild, or sea beet is said by Johnson (1862) to be woody and 'of no value as food to man nor cattle', an opinion shared by Grieves (1931). The use of the leaves of beets preceeded that of the roots though the latter varys greatly in woodiness and it is probable that the fleshier varieties of wild beet were used both medicinally and as food by the Romans prior to the development of domesticated varieties, (Ford-Lloyd and Williams 1975, Simmonds 1976).

POLYGONACEAE

Polygonum bistorta

The rootstock may be eaten raw or cooked (Morton 1963), Turner 1981). Rogers (1980) mentions the roasting of the roots of any of 20 species of Polygonum; both Johnson (1862) and Grievess (1931) mention the baking of bread from the root of the plant in both Russia and Siberia in times of scarcity. Uphof (1968) indicates a medical use as food by the Cheyenne Indians.

Rheum rhaponticum/Rheum palaestinum

Though known for the use as food of the fleshy petioles the medicinal use of the rootstock has been known for thousands of years and is well documented (Copper and Johnson 1984). Uphof (1968) states that the rootstock is dried prior to its use medicinally.

CUCURBITACEAE

Bryonia dioica

The medicinal use of the swollen root of this species has been mentioned by Johnson (1862), Grievess (1931), Guest

(1933), Eldin (1951) and Uphof (1968). It may be used as a drastic purgative, though Augustus Caesar also wore the plant around his head during thunderstorms to protect against lightening (Eldin 1951).

CRUCIFERAE

Crambe cordifolia

The root of this taxon is edible and according to Mueller (1891) quoted by Hendrick (1919), is known colloquially as colewort. He states that the 'root and foliage afford an esculent'.

Crambe maritima

Though not specifically the roots (though these are the only parts of the plant that would normally survive charring), the fleshy parts of the plant are eaten (Tanaka 1976).

PRIMULACEAE

Cyclamen persicum

The medicinal use of the storage organs of Cyclamen species is mentioned by Uphof (1968) and by Thompson

(1949). The latter also mentions the use as a form of soapwort.

ROSACEAE

Potentilla anserina

The use of the root as food of this species is well documented (Morton 1963, Norton 1981, Turner 1981). Potentilla anserina ssp. pacifica is an important wild resource of North West coast American Indians, (Turner and Kuhnlein 1892), commonly being cooked by steaming and used in the preparation of several dishes. Johnson (1862) mentions that the boiled and roasted root supported peoples of the Hebrides for months on end during time of famine.

LEGUMINOSAE

Lathyrus linifolius

Both this taxon and L. tuberosus are documented as having edible root tubers. Uphof (1968) states that the tubers of L. tuberosus may be boiled and eaten as a vegetable. Grigson (1958) states that the tubers of L. montanus (= L.

linifolius), may be eaten as a vegetable or used to flavour whiskey.

ONAGRACEAE

Oenothera biennis

The fleshy root of this species is said by Medsger (1939) to be edible and nutritious. Both Rogers (1980) and Morton (1963) state that the root may be eaten in late Autumn, Winter and Early Spring. Johnson (1862) states that its use as a kitchen garden plant decreased since the introduction of the potato, though remained popular for some time after in Germany.

GERANIACEAE

Biebersteinia multifida

Though literature pertaining to this particular species is not available the edibility of the vegetative organs of the Geraniaceae is well documented (Uphof 1968). Confirmation of its use in parts of the Near East await the results of further ethnographic studies by Miller et al (in Prep.).

Erodium glaucophyllum

Baillon (1878), quoted by Hendrick (1919) states that the tubers of Erodium species are eaten in Egypt. Tanaka (1976) also lists many Erodium species with edible tubers.

UMBELLIFERAE

Conopodium majus

The pignut is referred to by many authors as an edible tuber. Johnson (1862) mentions it as being nutritious and a resource used in times of scarcity. Grigson (1958) quotes John Pechey (1694) from his 'Complete herbal of Physical Plants' stating that the 'peeled nuts boiled in fresh broth and a little pepper were pleasant and very nourishing.....'.

Eryngium maritimum

The boiled or roasted root of this taxon is both palatable and nutritious according to Smith (1882). Though as a wild resource the root is more likely to be cooked in this way, in Europe during the 17th and 18th century the root was highly prized as a candied sweetmeat, known as 'eryngo' (Johnson 1862). The medicinal use of this root

for those that are 'liver sick' is cited by Grievess (1931).

Heracleum sphondylium

Johnson (1862) states that the roots of this species are used as animal fodder. The roots of Heracleum species in general (Tanaka 1976) and H. lanatum in particular (Uphof 1968) are said to be edible when cooked.

Myrrhis odorata

The root of sweet cicely may be eaten raw (Wren 1950), or boiled (Eldin 1951) and is stated by both Johnson (1862) and Grievess (1931), not only to be an excellent vegetable especially when eaten with oil and vinegar but also as a stimulant increasing in old people both 'lust and strength'.

GENTIANACEAE

Gentiana lutea

The medicinal action of the powdered root of this species is well documented, a popular recipe being given by Wren (1950). Uphof (1968) also mentions its use in the

manufacture of liquor as well as listing other Gentiana species with similar uses.

SOLANACEAE

Withania somnifera

The ancient Indian drug, Ashwagandha, is derived from the roots of this plant. It is a narcotic intended to improve strength and vigour being regarded as an aphrodisiac and rejuvenator, (Atal and Schwarting 1961). Uphof (1968) considers the use of the roots as a cure for diseases of the rectum.

BORAGINACEAE

Lithospermum erythrorhizon

According to Rogers (1980) the roots of several species of Lithospermum may be eaten when cooked though the roots of this species are also a source of dye (Uphof 1968). Uphof also states that other species of this genus are used medicinally.

Symphytum officinale

The medical use of this taxon is well documented, the powdered root being the ingredient of many herbal preparations (Uphof 1968). It acts as both an astringent and a demulcent. The leaves and young shoots of the plant are edible and recommended as an emergency food crop.

OROBANCHACEAE

Cistanche tubulosa

Orobanche species are eaten by many North American Indians (Rogers 1980); these may be eaten raw but are better roasted. Cistanche species are eaten in Africa and the Near East, C. lutea by the Touregs (Uphof 1968), and C. tubulosa by the bedwin of Sinai and the Negev (Bailey and Danin 1981). The latter is said to be roasted prior to eating.

COMPOSITAE

Anacyclus pyrethrum

The root is a source of an essential oil used in liquors, for mouth washes and for toothache. The fresh roots may

be chewed or dried and used in preparations (Potter 1950, Uphof 1968).

Arctium minus

The root of both this species (Rogers 1980) and Arctium lappa (Johnson 1862, Grieves 1931, Morton 1963, Uphof 1968), are edible raw after being peeled. It may also be boiled or dried and made into flour to thicken soups and stews.

Doronicum grandiflorum

Uphof (1968) gives medicinal uses for many Doronicum species as well as their use as a constituent of aromatic tonics.

Inula helenium

The root was used by the Romans both medicinally and as a condiment (Grieves 1931). It has been a source of Inulin and a sweet meat since. Uphof (1968) indicates a number of medicinal uses and its use as an ingredient in an aromatic tonic.

Saussurea lappa

The use of this root is well documented as a source of essential oil, as an aphrodisiac and medicinally against skin diseases (Uphof 1968).

Scorzonera judaica/Scorzonera schweinfurthii

Both S. schweinfurthii (Uphof 1968) and S. judaica (Bailey and Danin 1981) as well as other Scorzonera species are eaten in North Africa and the Near East. The tuberous roots are roasted prior to eating.

Taraxacum officinale

The roots of this species may be dug in Early Spring and eaten boiled or roasted and ground as a coffee substitute (Rogers 1980) or eaten raw (Morton 1963). The dried root may be used medicinally (Uphof 1968).

Tragopogon pratensis

Tragopogon roots may be eaten in a similar way to those of Taraxacum officinale (Rogers 1980), and are said by Grieves (1931) to have been eaten 'as we now eat parsnips'. T. porrifolius is a rather uncommon cultivated

root crop.

BUTOMACEAE

Butomus umbellatus

The rhizomes of this species are 'consumed as food by some peoples in Russia' (Uphof 1968). Hendrick (1919) quotes Unger (1859) as stating that the rhizome may be ground for flour to make bread and Johnson (1870) as stating that the rhizome may be roasted and then eaten. Lindley (1846) remarks that the rhizome is 'acrid and bitter' but may be 'eaten among the savages'.

ALISMATACEAE

Alisma plantago-aquatica/Alisma lanceolatum

The rootstock may be eaten fresh, though it has a strong taste, or may be used as a starch vegetable after drying (Rogers 1980). Grieves (1931) also states that the acidity of the rootstock is lost on drying and also that the powdered tissues may be employed by herbalists.

Sagittaria sagittifolia

The tubers of this taxon may be eaten raw, cooked or ground for flour, (Morton 1963). Rogers (1980), states that the boiled or roasted tuber dug in late Summer or Autumn has long been used as a food in Europe, China and North America. The plant is cultivated in China and Japan (Grieves 1931).

GRAMINEAE

Arrhenatherum elatius ssp. bulbosum

Ethnographic literature pertaining to the use of this species could not be found despite its frequent occurrence on archaeological sites (Parrington 1978, Heslop 1987).

Hordeum bulbosum

Guest (1933) states that the bulbous 'roots' of this species are edible and often eaten by children. Tanaka (1976) also states that the 'bulbs' are often eaten.

CYPERACEAE

Cyperus longus

The rhizomes of this species may be used in perfumery (Uphof 1968) or to make an aromatic tonic (Johnson 1862).

Cyperus rotundus

Many authors refer to the edibility of the small ovoid tubers of this species which may be eaten raw, fresh or dried (Guest 1933, Medsger 1939, Morton 1963, Uphof 1968).

Schoenoplectus tabernaemontani

Many Schoenoplectus species referred to in the literature under the synonym of Scirpus species other than those of the Scirpus maritimus group. Rogers (1980) mentions the use of Schoenoplectus rhizomes as food by the Lakota Indians of North America.

Scirpus maritimus

The edibility of the rootstock and rhizome of many Scirpus species is well documented by Morton (1963) and Turner (1981). The tissues may be eaten raw, baked or dried and

ground for flour (Rogers 1980). Heywood (1978) states that the tuber is eaten as a vegetable in China and Japan.

TYPHACEAE

Typha angustifolia/Typha latifolia

The rootstocks and rhizomes of this species may be boiled or roasted before eating or dried and pounded to make flour (Morton 1963, Rogers 1980). Extensive ethnographic details pertaining to this species are given by Morton (1975).

SPARGANIACEAE

Sparganium erectum

The 'bulbous stem bases' and 'tubers' of Sparganium species are edible when cooked (Rogers 1980) and according to Uphof (1968) are used as food by several American Indian tribes.

ARACEAE

Acorus calamus

The use of the rhizomes of this taxon is outlined by Rogers (1980). The dried rhizome has been used medicinally in Europe since Roman times. Small bits may be chewed for the juice which is swallowed or the rhizome may be grated into water which is then drunk as tea. The plant is collected in Autumn. They may also be candied as a sweetmeat or an oil may be extracted and used as a flavouring or moth repellent. According to Uphof (1968) the rhizomes are cultivated in Burma and Ceylon (Sri Lanka).

Arum maculatum

Both Johnson (1862) and Grievess (1931) state that the baked tubers of this species are edible and possibly nutritious. The roasted or boiled and subsequently pounded tissues yield a type of arrowroot largely made on the Isle of Portland and therefore known as 'Portland Arrowroot'. Soap, facial cosmetic and clothing starch have also been derived from the tuber of Arum maculatum (Johnson 1862).

IRIDACEAE

Crocus sativus

Crocus species may be used as a source of the dye 'saffron' (Grieves 1931), and also as a vegetable (Darlington and Wylie 1955).

LILIACEAE

Asphodelus aestivus

According to Uphof (1968) and Tanaka (1976) the swollen roots of a number of Asphodelus species are eaten as a vegetable.

Polygonatum X hybridum

The rhizome of a number of Polygonatum species is employed as an emergency food. Rogers (1980) states that the rhizome of P. biflorum may be added to stews or eaten like potatoes. Johnson (1862) states that the 'roots' macerated in water for some time yield a substance 'capable of being used as food and consisting principally of starch'. The garden hybrid variety is used for examination here due to the rarity of the wild British species.

DIOSCOREACEAE

Tamus communis

Coursey (1967) states that the yam-like tuber of this species is edible though prolonged boiling and soaking is necessary to remove toxins. He goes on to say that during prehistoric times and possibly medieval times the tuber was used as human food in Europe. Coursey offers no evidence other than citing Bois (1927), a French study of plants useful to man, largely taken from Gerrard's herbal (1633). It is quite possible that the tuber was used in a manner similar to that of many yams though its suggested use in prehistoric times lacks much in the way of solid evidence.

ORCHIDACEAE

Orchis mascula

The production of 'salep' from the dried root tubers of Orchis species and other members of the Orchidaceae is well documented. Johnson (1862) states that the starchy material called Bassorin, derived from the tubers is extremely nutritive and may be made into a drink.

CHAPTER THREE - ANATOMY, MORPHOLOGY AND CLASSIFICATION OF VEGETATIVE PARENCHYMATOUS ORGANS

3.1 INTRODUCTION

There is relatively little published work on the anatomy and morphology of vegetative parenchymatous organs compared with other plant organs because they are less accessible and little used in taxonomy. This is true of both the purely descriptive literature and of the more taxonomic or systematic literature. The majority of literature that does exist has been published largely as a result of research carried out between the 1920s and 1950s.

Early work dealing with the problems of defining morphological and anatomical terms and describing, in detail, the developmental anatomy of vegetative parenchymatous organs may be typified by that of de Bary (1884) and later Sablon (1902). In the early years of the 20th century the development of more technical equipment and a greater understanding of the importance of anatomical characters for systematic purposes, (Fritch 1903), led to detailed studies of individual taxa or groups of taxa. Several of such monographs were published between the 1920's and the 1950's. Though many

of these dealt with the fleshy secondary 'tap roots' of economically useful plants a few dealt with the fleshy vegetative structures of no economic importance. These however, form a minority.

The work of Artschwager (1926) on Beta vulgaris, Warning (1934) on Pastinaca sativa, Leon (1935) on Tragopogon porrifolius and (1939) on Daucus carota, Esau (1940) on Daucus carota and Knobloch (1954) on Cichorium intybus are outstanding examples of monographs illustrating the bias towards research on fleshy secondary root anatomy of economically useful plants. Hayward, (1948) in a collection of monographs on the anatomy of economic plants also serves to illustrate the nature of this research carried out in the first half of this century.

The work by Sablon (1902) on Tamus communis, Reed (1910) on Solanum tuberosum and Helianthus tuberosus, Artschwager (1924) also on Solanum tuberosum and Sharman (1938) on Orchis mascula serve to illustrate the more limited work on organs other than secondary roots.

There is a large body of published research concerning the three dimensional shape of parenchyma cells, often taking a highly theoretical stance. This work is important in demonstrating the structure and organised nature of

parenchyma, though considering the destructive effects of charring upon such tissues the relevance of this work is limited. Early observations by Hooke (1665) and Grew (1682) noted a similarity between parenchymatous tissue and 'congeries of very small bubbles'. Such observations continued with Mirbel (1802) and Kieser (1915) who examined the three-dimensional shape of cells and considered their frequent hexagonal appearance in cross section. Berthold (1886) and Errera (1887) realised the importance of 'surface tension in cellular systems'. Much of this early work considered typical cells to have twelve faces and it is only a few authors, such as Bernhadi (1805), Ducharte (1867) and most importantly Lord Kelvin (1887) who considered fourteen sided cells. Kelvin's orthic tetrakaidecahedron, having eight hexagonal and six square faces, or an approximation or modification of this permits the most economical surface-volume division of space. The combination of perfect orthic tetrakaidecahedra has no interstices. Though a few researchers still preferred a twelve sided model well into the twentieth century (Thompson 1917) most future research was based on the fourteen sided model.

Early extensive research and publication by Lewis (1923, 1925, 1928a, 1930) led to great interest in this area. Further research including that of Marvin (1939), Matzke

(1939, 1946) Marvin and Matzke (1939), Lewis (1943a, 1943b, 1944) and Dodd (1955) developed the highly theoretical approach towards the examination of cell shape using lead shot, soap bubbles and wax.

Higginbotham (1942) and Hulbary (1944, 1948) have examined the fresh parenchyma of root, leaf and petiolar tissue in their researches towards an appreciation of cell shapes.

More recently Korn and Spalding (1973) and Korn (1974) developed geometric and algebraic models to examine cell shape and the spatial relationships of cells during tissue growth.

A separate, though more limited, body of research has examined the role of air spaces in plant tissues, especially in that of aerenchyma. Sifton (1945, 1947) has presented a major review of this research and Armstrong (1972) has examined a functional aspect of aerenchymatous tissue.

In only one case has research been carried out on the vegetative parenchymatous tissue of a large fleshy storage organ, (Hulbary 1948). Here the cells of the tuberous roots of Asparagus sprengeri were examined and compared with those of the leaf of Rhoeo discolor. It was

concluded that the roots had a higher percentage of parenchyma cells with pentagonal faces whereas leaf cells had mostly hexagonal faces. Various configurations of face numbers and shapes for root and leaf cells were described.

This chapter contains a review of the relevant botanical literature dealing with, firstly, the classification of morphology, secondly the anatomy and finally infraspecific variation in vegetative parenchymatous organs.

3.2 THE CLASSIFICATION OF VEGETATIVE PARENCHYMATOUS ORGANS

3.2.1 Introduction

Several plant morphologists have attempted to tackle the problem of defining morphological categories of vegetative parenchymatous organs. General disagreement and apparent unwillingness to accept ill-defined terminology has led to an extreme state of confusion. Terms such as 'rhizome' and 'rootstock' have been defined differently so many times that it is often difficult to know what is meant if the terms are used without qualification. There are some organs whose morphological description will not match that of any definition. The problem is further complicated

when descriptive terminology is derived from the use of colloquial names. For instance, the tuber formed by the swelling of a lower internode of the vertical axis of Arrhenatherum elatius ssp. bulbosum is often wrongly termed a bulb, the common name of the plant being 'Onion Couch'.

Some early workers recognised the importance of morphological definitions of root, stem and leaf, and tried to produce a workable terminology with which to define plant forms. These included Mirbel (1815), de Candolle A.P. (1827, 1844), Lindley (1832), Bischoff (1833), de Candolle A. (1835, 1880), Gray (1879) and Bois (1893). This early interest in plant morphology was re-awakened after the First World War with work by Gatin (1924), Artschwager (1925) and Hayden (1919). The latter made the important step of outlining the function of vegetative parenchymatous organs; these being storage, anchorage, absorption, conduction and propagation. Perennation was not mentioned. Functions have played an important part in the definition of morphological terms. Hayden also, without actually defining specific morphological categories states that Typha latifolia has a horizontal rootstock while Phragmites communis has a creeping rhizome. This presents no small amount of confusion since both appear morphologically similar. The

rhizome/rootstock terminology has never satisfactorily been developed to an extent that will prevent either confusion or contradiction. Holm (1929) was in favour of a very much generalised definition of the term rhizome allowing it to cover organs that were horizontal or vertical, homogeneous or heterogeneous, monopodial or sympodial, rooting or rootless. He examined combinations of these character states giving examples of each. Aeschumann and Bocquet (1980) thought that the term rhizome covered too wide a range of morphological types and therefore required limitation. The authors wished to reserve the term 'geocorm', used by Du Reitz (1931), for any underground stem, replacing rhizome in its wider sense as used by Holm (1929). This term was then subdivided to include the term rhizome in a much stricter sense. This, however, seems inconvenient since the term rhizome should possibly define organs more varied than that covered by the definition outlined by Aeschumann and Bocquet though the term could be used in a stricter sense than that outlined by Holm. An overall term, such as 'geocorm', covering many varied definitions often separates morphologically similar groups of organs that would otherwise be classified together. For instance, rhizomes may occur above or below ground; under the classification outlined by Aeschumann and Bocquet some will be defined by the term 'geocorm' and others not.

The difference between rhizome in its strict sense and the 'stolon' is, according to Traub (1973), that the former is an underground organ and the latter above ground. Both form roots and shoots at nodes for the purpose of propagation, neither storage nor perennation were mentioned. Intermediates such as the rhizome/stolon of Iris species are mentioned to stress the importance of recognising the overlap between the terms. Traub's definitions are not employed here.

The restriction of the term rhizome to a modified horizontal or, in certain cases, vertical stem leads to a requirement of a different term for similar swollen vegetative organs with a vertical orientation but without the characteristic rhizomatous morphology. Various terms have been suggested; pseudo-rhizome by Nilsson (1882-1883), rootstock and caudex by many plant morphologists, the latter recently by Aeschmann and Bocquet (1980). The terminology covers a wider range of organs ranging from the massive structure in Tamus communis derived from the swelling of the first epicotyledonary internode (Ayensu 1972), to the swollen lower internodes of grasses such as Hordeum bulbosum and Arrhenatherum elatius ssp. bulbosum. This also includes the swollen stem bases of Alisma plantago-aquatica and Polygonum bistorta.

The very varied nature of parenchymatous organs derived from stem tissue, resulting from the presence of nodes and varied orientation, has always caused more confusion in attempts to develop a descriptive terminology than have vegetative parenchymatous organs derived from root tissue. Cannon (1949) stated that there is no satisfactory classification of root systems though its usefulness in classification of organ types would be open to question if one did exist. Storage root organs are easily classified into tubers, where swollen regions of root tissue exist as part of a much narrower root system, and swollen roots where the whole root is fleshy though slender lateral roots may also exist.

3.2.2 Morphological Definitions

Throughout the research presented here a classification of vegetative parenchymatous organs has been used which has been drawn up from a combination of previously published classifications and other observations. This is divided into three groups, vertically oriented stem tissues, horizontally oriented stem tissues and root tissues. The classification is outlined in diagrams 3.1, 3.2 and 3.3.

Vegetative parenchymatous organs are divided here into those derived from stem tissue and those derived from root

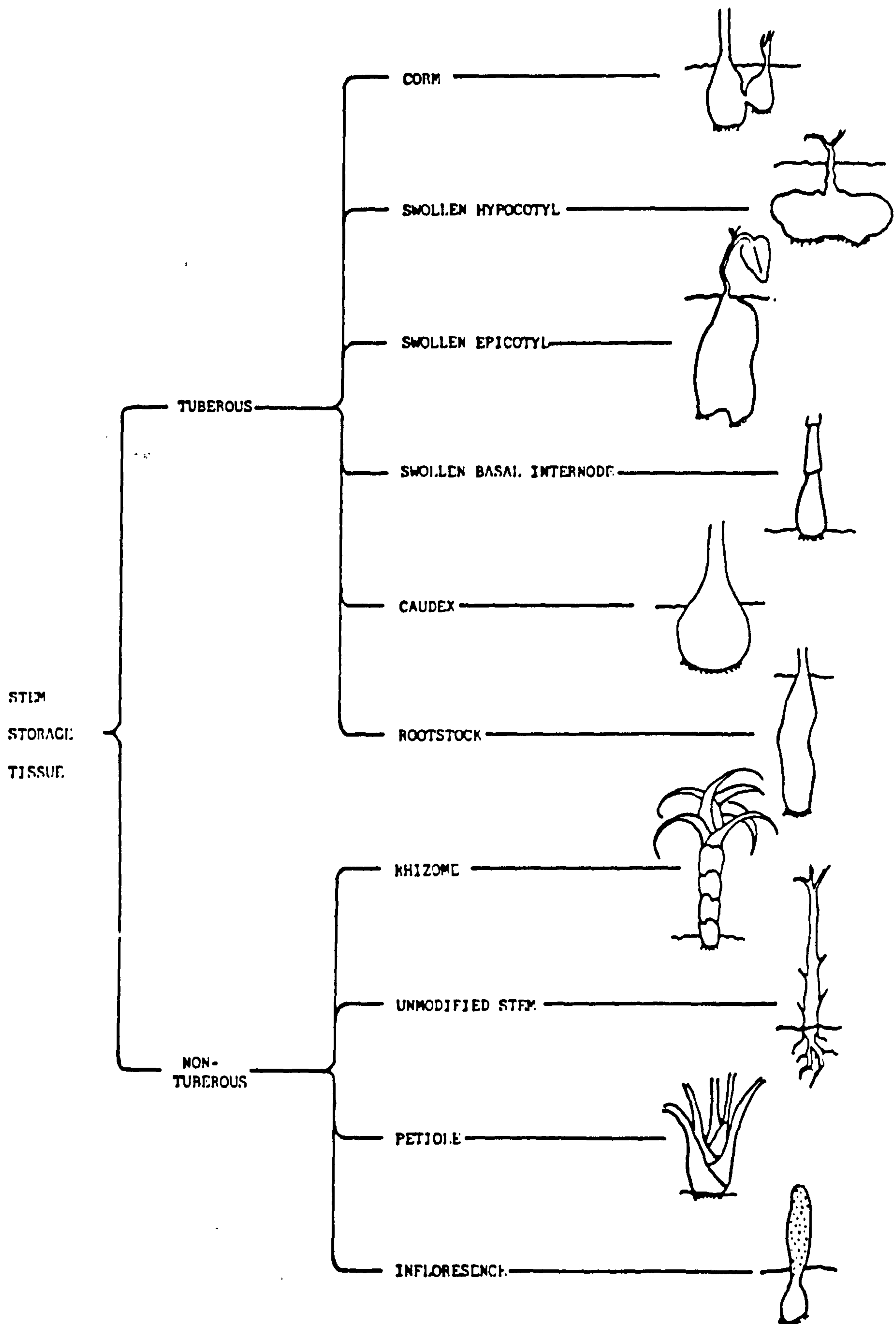


DIAGRAM 3.1 MORPHOLOGICAL CLASSIFICATION OF STEM AND LEAF STORAGE ORGANS - VERTICAL ORIENTATION

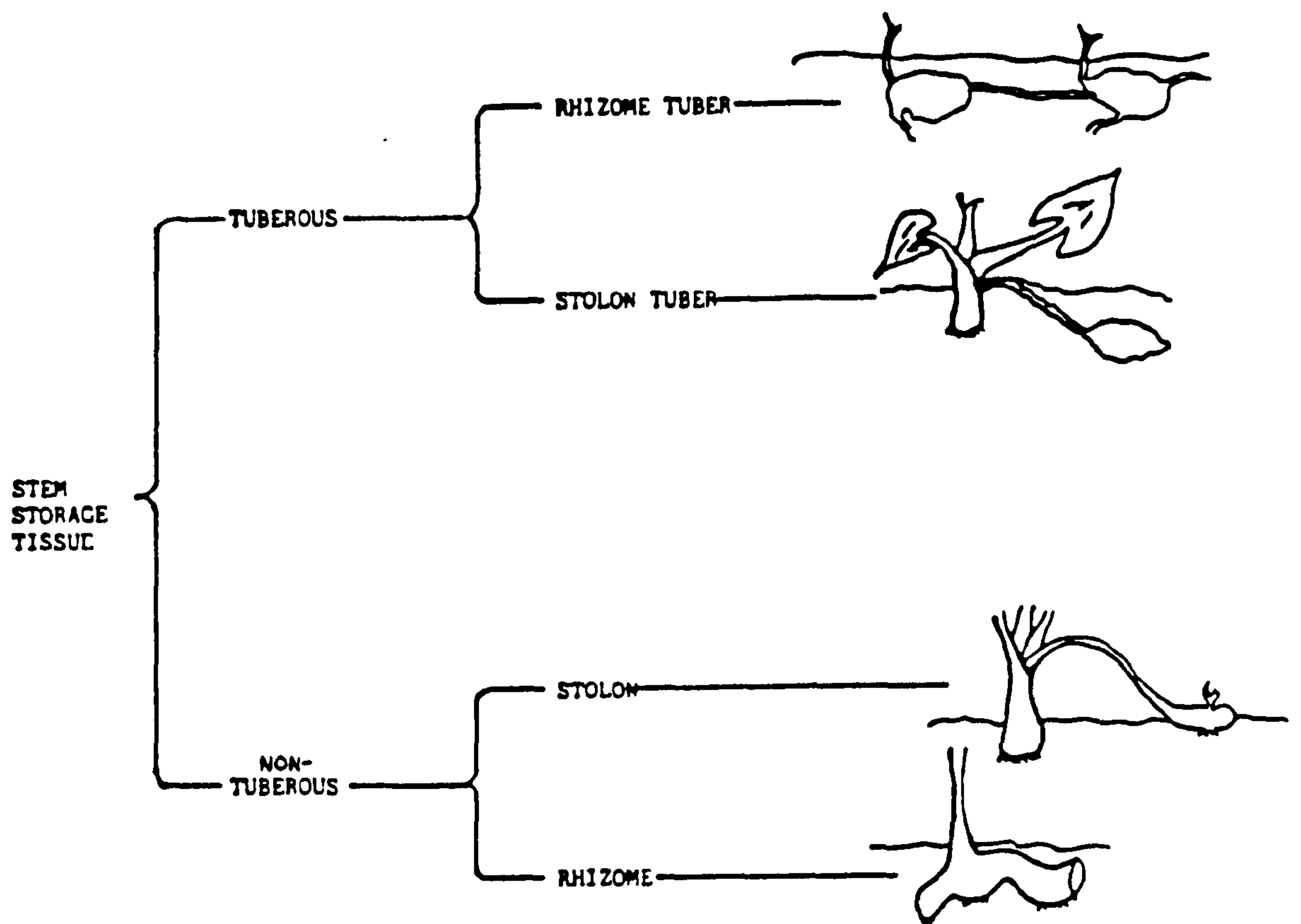


DIAGRAM 3.2 MORPHOLOGICAL CLASSIFICATION OF STEM TISSUE STORAGE
ORGANS - HORIZONTAL ORIENTATION

tissue. Organs derived from stem tissue are then subdivided into those of vertical and those of horizontal orientation. Those with horizontal orientation are divided into tuberous and non-tuberous rhizomes and stolons. Those with vertical orientation are divided into

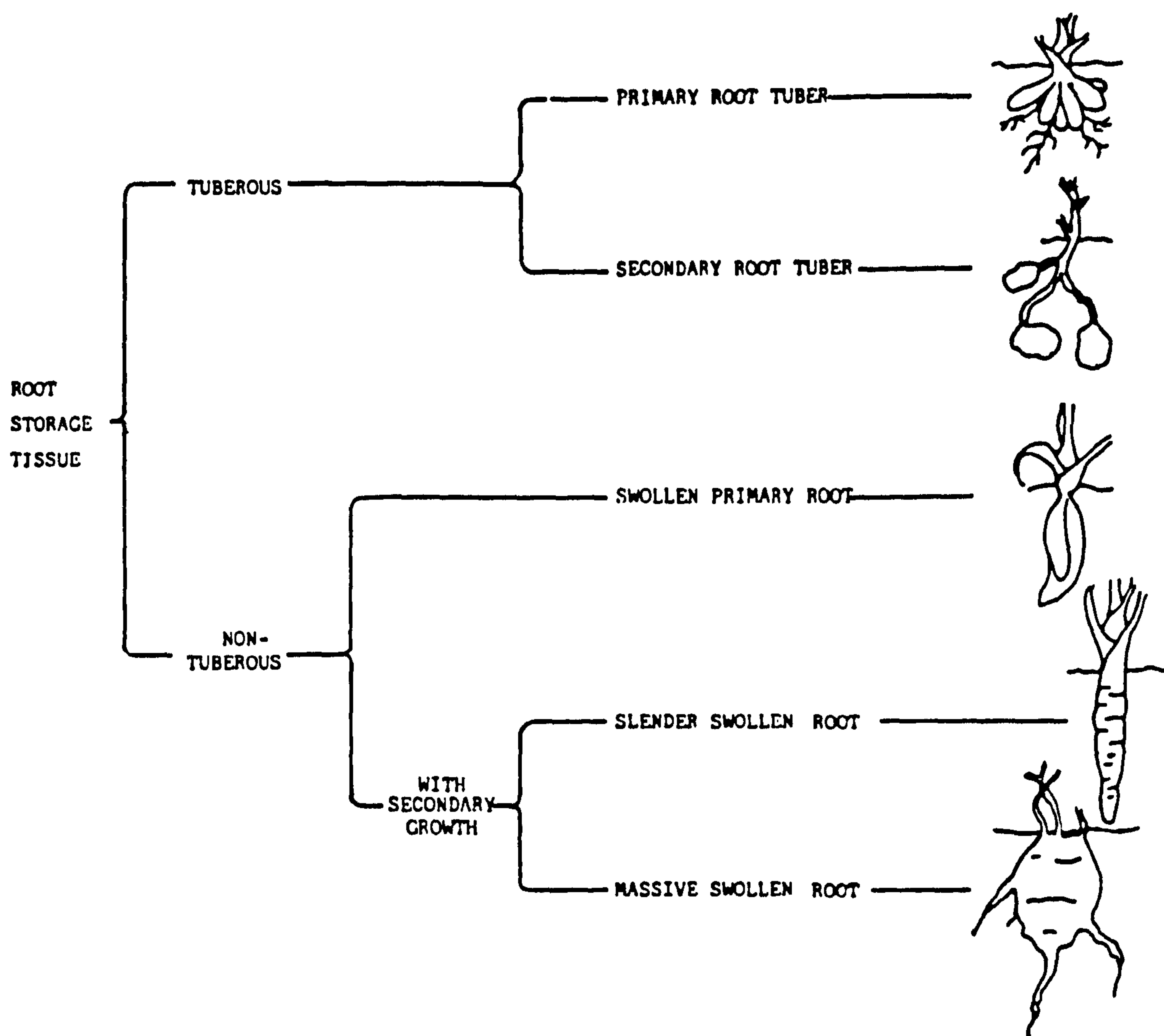


DIAGRAM 3.3 MORPHOLOGICAL CLASSIFICATION OF ROOT TISSUE STORAGE ORGANS

those with a tuberous and a non tuberous nature. Each of these is then divided into a number of morphological types.

Organs derived from root tissue may be classified simply by separating root tubers from completely swollen roots. These may both then be subdivided into those composed of primary and secondary tissues. Secondary swollen roots may be further divided into those of a slender or massive nature.

It is noted that vegetative organs covering a wide range of developmental morphologies may all be colloquially termed 'tuber'. Such is the case with the swollen hypocotyl of Cyclamen persicum, the swollen epicotyl of Tamus communis, any of the many rhizomes, stolons and root tubers and the massively swollen root of Bryonia dioica. While I have attempted to avoid this type of generalised colloquial terminology, unless developmental studies are made this is often not possible.

In understanding the classification of vegetative parenchymatous organs their functional morphology may be considered. Holm (1925) states that fleshy 'tap roots' are often organs of biennial perennation in dicotyledenous plants, and do not occur in monocotyledons. This is an important morphological consideration and is evident on the examination of the anatomy of the secondary root growth of such organs. The function of fleshy vegetative organs was investigated by Hayden (1919). He suggested

ORGAN TYPE	PERENNATION	VEGETATIVE REPRODUCTION	ANCHORAGE	ABSORPTION (CONDUCTION)	STORAGE
<u>STEM</u>					
CORM	X	X	X		X
SWOLLEN HYPOCOTYL	X		X		X
SWOLLEN EPICOTYL	X		X		X
SWOLLEN BASAL INTERNODE	X	X			X
STOLON		X			X
STOLON TUBER	X	X			X
RHIZOME	X	X	X		X
RHIZOME TUBER	X	X			X
CAUDEK	X		X		X
ROOTSTOCK	X	X	X		X
VERTICAL AERIAL AXIS					X
SWOLLEN INFLORESCENCE					X
SWOLLEN PETIOLE					X
<u>ROOT</u>					
PRIMARY ROOT TUBER	X			X	X
SECONDARY ROOT TUBER	X			X	X
PRIMARY STORAGE ROOT	X		X	X	X
SECONDARY STORAGE ROOT					
- SIMPLE	X		X	X	X
SECONDARY STORAGE ROOT					
- MASSIVE	X		X	X	X

TABLE 3.1 THE FUNCTIONAL MORPHOLOGY OF VEGETATIVE PARENCHYMATOUS ORGANS

storage, anchorage, absorption and conduction, and propagation as a list of functions. However perennation, distinguishing a non-perennating function of a storage organ was omitted.

Table 3.1 presents each of the organ types together with

their functions summarised under the five headings, perennation, vegetative propagation, anchorage, absorption (conduction) and storage.

Each of the morphological types outlined in diagrams 3.1 and 3.2 are described in detail below.

Corm: This is a vertical, multinodal swollen stem base ranging from spherical or ovoid to circular and dorsoventrally flattened. Some corms are annual persisting below ground while the aerial parts die seasonally. The base of the corm of Crocus spp. supports a fibrous root system. Here the corm lives for the duration of one year, giving rise from axillary nodal buds to new corms, during the growing season. The old corm withers and dies but there is a direct relationship between new and old corms. In Colocasia spp. adventitious roots occur all over the corm but are more highly concentrated at the shoot end. Axillary corms appear at nodes but these may co-exist with the parent corm, (Younghen 1919). The central corm is often more than one year's duration. These two corm types reflect seasonality in their respective temperate, and sub-tropical to tropical habitats. The ability to multiply vegetatively is an important criterion in the morphological distinction between the corm and the superficially similar caudex type

rootstock. The two have the functions of anchorage, perennation and storage in common.

Swollen Hypocotyl: This is vertically oriented swollen tissue derived from the hypocotyl, the region of stem between the root/shoot junction and the first true node. In Cyclamen persicum a fibrous root system emerges from the base, and shoots from the flattened upper surface. Though circular in transverse section the organ is somewhat dorsoventrally flattened. Functionally the swollen hypocotyl acts as an organ of perennation and storage but not of propagation, (Denffer 1894). The distinction has to be made between many cultivated 'tap roots' which are part hypocotyl and part secondary root and the swollen hypocotyl as a distinct organ as exemplified by Cyclamen persicum. In the latter there is a morphological distinction between the stem and the root, whereas in the former they merge.

Swollen Epicotyl: The massively tuberous perennating organ of Tamus communis is derived from the swelling of the first epicotyledonary internode of the seedling, (Ayensu 1972). The process of tuberization results in an organ that is massive and irregular in shape though elongated vertically, and with shoots from its upper surface; it is partially covered in adventitious roots. Similar to the

hypocotyl of Cyclamen persicum the organ is derived from the tissue of a single internode and so lacks any axillary buds. The organ is therefore incapable of propagation but acts as an organ of anchorage, perennation and storage.

Swollen Basal Internode: Typical of members of the Gramineae this organ is composed of vertical stem tissue derived from a single internode. A single plant made up of a number of shoots connected by horizontal stem tissue may contain a number of swollen basal internodes. The swelling occurs either at the lowest vertical internode or at one close to the base of the vertical axis rather than at the lowest internode of the whole stem. Hordeum bulbosum and Arrhenatherum elatius ssp. bulbosum are examples of this type of growth habit. In themselves these swollen internodes are not capable of vegetative multiplication, but since they often root at the lower node, any that split away from the parent plant will continue to grow therefore propagating the plant. The swollen internodes act as organs of storage and perennation above ground while the shoots above the swollen nodes die away seasonally.

Stolon: A stolon is an aerial or subterranean axis branching from the main axis, often with long internodes that, if aerial, cannot support its own weight and so

bends towards the ground. This is distinct from a runner which is a creeping axillary stem occurring above the ground, rooting and shooting at nodes. A stoloniferous plant is distinct from one that may be termed rhizomatous in that the main body of the plant still forms the centre of growth and has the ability to maintain apical dominance over the growth of stolons. Rhizomatous growth differs from this and is described below. The aerial stolon roots and shoots at nodes that touch the ground when the axis bends though both roots and shoots may form partially, before the stolon touches the substrate. Doronicum grandiflorum forms a stolon that is homogeneously fleshy along the length of the axis. Heterogeneous swelling along the length of the stolon, leading to the formation of stolon tubers, is described below. A stolon may be narrow rather than fleshy in which case the function of the organ is purely propagation. The fleshy stolon of Duronicum grandiflorum has the additional function of storage.

Stolon Tuber: The stolon, as described above, may be narrow and either terminate in, or have along the length of the axis, swollen regions of usually more than one internode. Sagittaria sagittifolia has a terminal tuber (Winton and Winton 1935). This acts as an organ of perennation, propagation and storage but not anchorage.

Morphologically the underground storage tubers of Solanum tuberosum are stolon tubers formed along the length of narrower underground stolons radiating out from the main central vertical underground axis of the plant. Both Artschwager (1924) and Hayward (1948) state that the structures may be interpreted as rhizome and rhizome tuber. Reed (1910) interprets the structure as stolon and stolon tuber. The present study follows the view taken by Reed, that the underground stem structures of Solanum tuberosum are stolon and stolon tuber. This view will be taken for analogous structures, the term rhizome and rhizome tuber restricted to the definition and description outlined below.

Rhizome: This is a multinodal, wholly or partially subterranean, more or less homogeneously swollen or unswollen stem structure horizontally or vertically oriented. It may be narrow and long, truncated, branched or unbranched, monopodial or sympodial. Horizontal rhizome morphology varies greatly from the relatively simple rhizome of Anemone nemorosa (Bell and Sherrifs 1984), with long internodes, to the truncated rhizome of Nymphaea alba, (Cutter 1957) or to the complex branching pattern of Alpinia species (Bell 1979). Rhizomes often advance from a growing tip and die at the opposite end. A horizontal rhizomatous stem system often has shoots

arising vertically at nodes. There is no central organization to the plant. Differing from this the stolon is an axillary branch arising from a plant with a central vertical organization. Vertical rhizomes such as those of Prionium (Juncaceae) and Xanthorrhoea species (Xanthorrhoeaceae) grow vertically from an apical bud but still produce shoots and flowering axes from lateral buds. The rhizomes themselves are characteristically truncated.

Rhizome Tuber: In a similar way to stolon tubers, rhizome tubers form as heterogeneously swollen regions, terminally or along the length of narrower horizontal rhizomes. These are storage perennating and propagating structures; examples are Cyperus rotundus and Cyperus esculentus described by Garg, Bendixen and Anderson (1967).

Rootstock: The term rootstock is highly misleading since such organs are modified stems. While it would be desirable to replace the term with a more apt word it is felt that it is so entrenched in the botanical terminology that the introduction of yet another term would cause even more confusion. The rootstock is a vertically oriented swollen stem base multinodal and other than spherical in shape. It occurs at the base of a vertical or near vertical axis. Examples of these are the rootstocks of Polygonum bistorta, Dryopteris felix-mas or Arum maculatum.

The latter is described by Winton and Winton (1935). These structures are mostly non-propagating though may produce rhizomes from nodal buds, perennating and may persist for a number of years.

Caudex: Similar in many respects to a corm this is a rootstock, being multinodal, swollen, vertically oriented stem tissue occurring at the base of a vertical or near vertical axis. It is always rounded, similar in shape to the corm of Crocus spp. but differs in that it is unable to propagate by the production of new corms from axillary buds. It may form as part of a complex of rhizomes and rhizome tubers where its functions are perennation, storage and anchorage. An example of this is Sparganium erectum. The caudex may occur as a solitary structure forming a single perennating organ such as in Alisma plantago-aquatica. It is interesting to note that in describing the perennating structure of Alisma, Lieu (1979) uses the phrase 'short upright stem', while Tomlinson (1969) 'short erect corm' and Stant (1964) 'a bulb-like structure'. While Lieu is correct in the description of the structure the chosen phrase is vague. The terms used by Tomlinson and Stant are, in this study, restricted to other morphological structures and so cannot be used to describe the perennating structure of Alisma.

Vertical Aerial Axis: Some vertical stems may become fleshy though not necessarily swollen or tuberised, and act as organs of storage. By definition these are not perennating structures since they die seasonally, perennating by other methods, continue to grow throughout the year or are short lived.

Swollen Inflorescence Axis: The inflorescence axes of some plants may become fleshy and although their primary function is one of floral display and support these also contain large masses of parenchymatous tissue. The morphology and anatomy of these structures varies greatly. Under study in the present research is the swollen inflorescence axis of Cistanche tubulosa.

Swollen Petiole: The petioles of some taxa act as storage organs becoming swollen and fleshy. In areas with marked seasonality the aerial parts of biennial or perennial taxa die seasonally. Examples of such taxa are Apium graveolens and Rheum rhaponticum. In areas where seasonality does not exist or is limited storage petioles may be perennial.

Primary Root Tuber: Any heterogeneously swollen region of a root or entirely swollen root occurring directly below the stem root junction may be called a root tuber if it

co-exists with a narrow root system. Generally its function is storage and perennation. The narrow root system carries out the function of anchorage and absorption. Roots of monocotyledons and dicotyledons that have not undergone secondary growth are composed of primary tissues. These may be typified by two morphologically similar structures, though anatomically these are very different. Ranunculus ficaria has a cluster of short swollen primary roots directly below the transition zone at the root/shoot junction. These are widest at a point two thirds away from the proximal end and rounded at the distal end. They are narrow at their point of attachment. The surface of these tubers is featureless. Orchis mascula has two larger tubers below the root/shoot junction, one being recent and the other of the previous season. One is fully swollen and the other somewhat shrivelled. The tubers are ovoid in shape though vertically flattened. Again the surface is featureless. Both these structures are similar in being simple swollen primary roots attached directly below the root/shoot junction.

Secondary Root Tuber: Dicotyledons that have undergone secondary growth and form what may be identified anatomically and morphologically as root tubers are represented in this study by Lathyrus linifolius and

Conopodium majus. The former supports swollen spherical or near spherical tubers along the length of an almost fibrous root system. The latter has a single spherical tuber at the base of the stem below the transition zone that gives rise to fibrous roots.

Primary Swollen Root: Fundamentally similar to the root tubers of Ranunculus ficaria the swollen roots of Asphodelus aestivus may be differentiated morphologically in that the swollen roots form the whole of the root system. The tubers of Ranunculus ficaria form a cluster of root structures separate from a well defined unswollen root system. The swollen roots of Asphodelus aestivus are narrow at their point of attachment, generally cylindrical throughout their length and acutely pointed at their distal end. There may be many on each plant.

Secondary Swollen Roots - Slender: The swelling of the primary root at the expense of the lateral roots is typical of the secondary growth of many biennial and perennial plants. These laterals often remain narrow and fibrous. The swollen primary root or 'tap root', specialized for storage and perennation, may be a single straight axis as in Daucus carota, occasionally branched as in Pastinaca sativa or highly ramified as in Beta vulgaris ssp. maritima.

Secondary Swollen Roots - Massive: When the development of a swollen primary root goes beyond the point where the shape of the root as a branched or unbranched tapering structure is obvious by the process of more or less irregular tuberisation this results in an often massive irregular root. This often supports narrow lateral roots. It acts as a storage and perennating organ possibly persisting for many years. The root of Bryonia dioica is similar to this, being an irregular tuberous organ giving rise to a number of shoots from a flattened upper surface.

3.3 THE ANATOMY OF VEGETATIVE PARENCHYMATOUS ORGANS

3.3.1 Introduction

In this section brief examination of the important anatomical features relating to the understanding of the morphological types described above is presented. This reflects the major dichotomy of morphological categories into organs derived from either root or stem tissue. The organization of these tissues in terms of the origin and the position of the storage parenchyma will be described. The following is not meant as an all encompassing guide to the anatomy of vegetative parenchymatous organs but more as a guide to the more salient points relevant to the

following chapters of results. In describing the anatomy of vegetative parenchymatous organs in general, specific examples are drawn from literature concerning the taxa under observation in this research.

3.3.2 Stem Tissue

Though a generalization, it is possible to divide patterns of tissue organization into a number of different forms dependant on which zones of the stem have given rise to regions of parenchyma in relation to the position of vascular and endodermal structures. This is outlined in Diagram 3.4

Stem tissues with a monocotyledonous vascular organization may be divided into those with and those without an endodermis or analogous structure. The apparent random and diffuse vascular bundle organization of the atactostele occurring throughout the organ, uninterrupted by an endodermis is typified by the rootstock of Arum maculatum. When an endodermis, endodermoid sheath or analogous structure is present, development of wide regions of parenchymatous or aerenchymatous tissue may occur in the cortex and in the stele or solely in the stele, the cortex then being narrow. Cyperus rotundus tubers are an example of the former and the rhizomes of

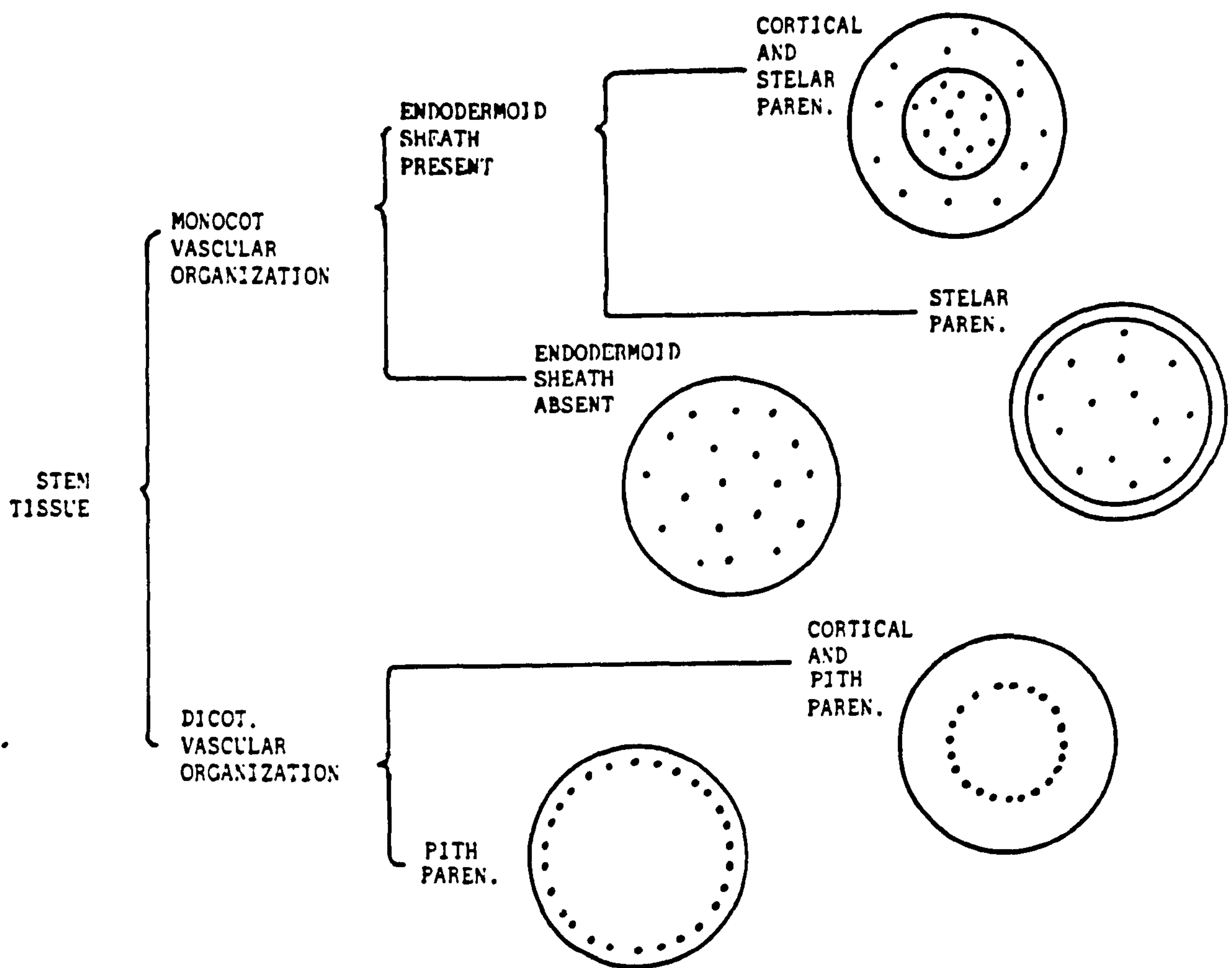


DIAGRAM 3.4 ORGANIZATION OF STEM TISSUES IN SELECTED FORMS
(SHOWN IN TRANSVERSE SECTION)

Butomus umbellatus an example of the latter.

Intermediates also occur where parenchymatous tissue is developed in both the stele and the cortex, but where these regions may not be equal.

Primary dicotyledonous stem vascular structure appears

more organized, vascular bundles forming a hollow cylinder, seen as a ring (normally single) concentric with the epidermis in transverse section. The position of the vascular tissue relative to the epidermis leads to different width ratios of parenchymatous tissue in the cortex and pith. An example of where the vascular tissue divides the parenchymatous tissue of the cortex and pith equally is found in the rhizome of Anemone nemorosa. Where the vascular tissue lies close to the epidermis, the majority of the parenchymatous tissue of the organ lies within the pith. This is typified by the rootstock of Polygonum bistorta.

Though morphologically varied, structures derived from stem tissue may have certain anatomical features in common. This may be seen in plants such as Scirpus maritimus and Sparganium erectum where the stem system is composed of a complex system of rootstocks, rhizomes and rhizome tubers. Here the anatomy throughout is similar, the only differences reflecting the morphological situation of the organ.

The vascular tissue of a transversely sectioned organ may appear to be in either transverse or oblique section whether it is of monocotyledonous or dicotyledonous organization. In the tissues under observation, the

oblique and apparently random arrangement of the vascular bundles is a character resulting from either of two phenomena.

Firstly, the tuberization of internodal organs such as Tamus communis, which results from the swelling of the first epicotyledonary internode, (Ayensu 1972). Originally, prior to tuberization, the vascular tissue would run parallel to the longitudinal axis of the stem. Tuberization leads to the distortion of this relatively simple vascular system, causing it to appear oblique in section when the organ is sectioned transversely.

Secondly, the truncated nature of some multinodal organs leads to an obliquely placed and often highly contorted system of vascular bundles. This results from the close positioning of nodes and the vascular traces leading to them. The horizontal tissue of the rhizome of Nuphar advena and the vertical tissue of the caudex of Alisma plantago-aquatica both display this character.

The vascular tissue of internodal organs that are not massively tuberous such as the swollen internodes of the grasses Hordeum bulbosum and Arrhenatherum elatius ssp. bulbosum and multinodal organs with long internodes such as Typha latifolia and Anemone nemorosa tends to run

parallel to the long axis of the organ. Both the organ and the vascular tissue within it will be cut transversely in transverse sections.

3.3.3 Root Tissue

As with stem tissue, it is possible to divide root tissue anatomy into a number of generalised types based on the position of the parenchymatous tissues. These are illustrated in Diagram 3.5 and for dicotyledons described below.

The primary organization of fleshy root tissues is illustrated in figure one of diagram 2. Here a tetrarch root is shown. The cortex of the root, between the endodermis and the epidermis, may become swollen and act as storage tissue. This occurs in the root tubers of Ranunculus ficaria and are described by Hacket, (1927).

KEY TO DIAGRAM 3.5 (PAGE 110)

x = xylem	Ep = epidermis
Ph = phloem	c = cambium
Pc = pericycle	p = periderm
En = endodermis	

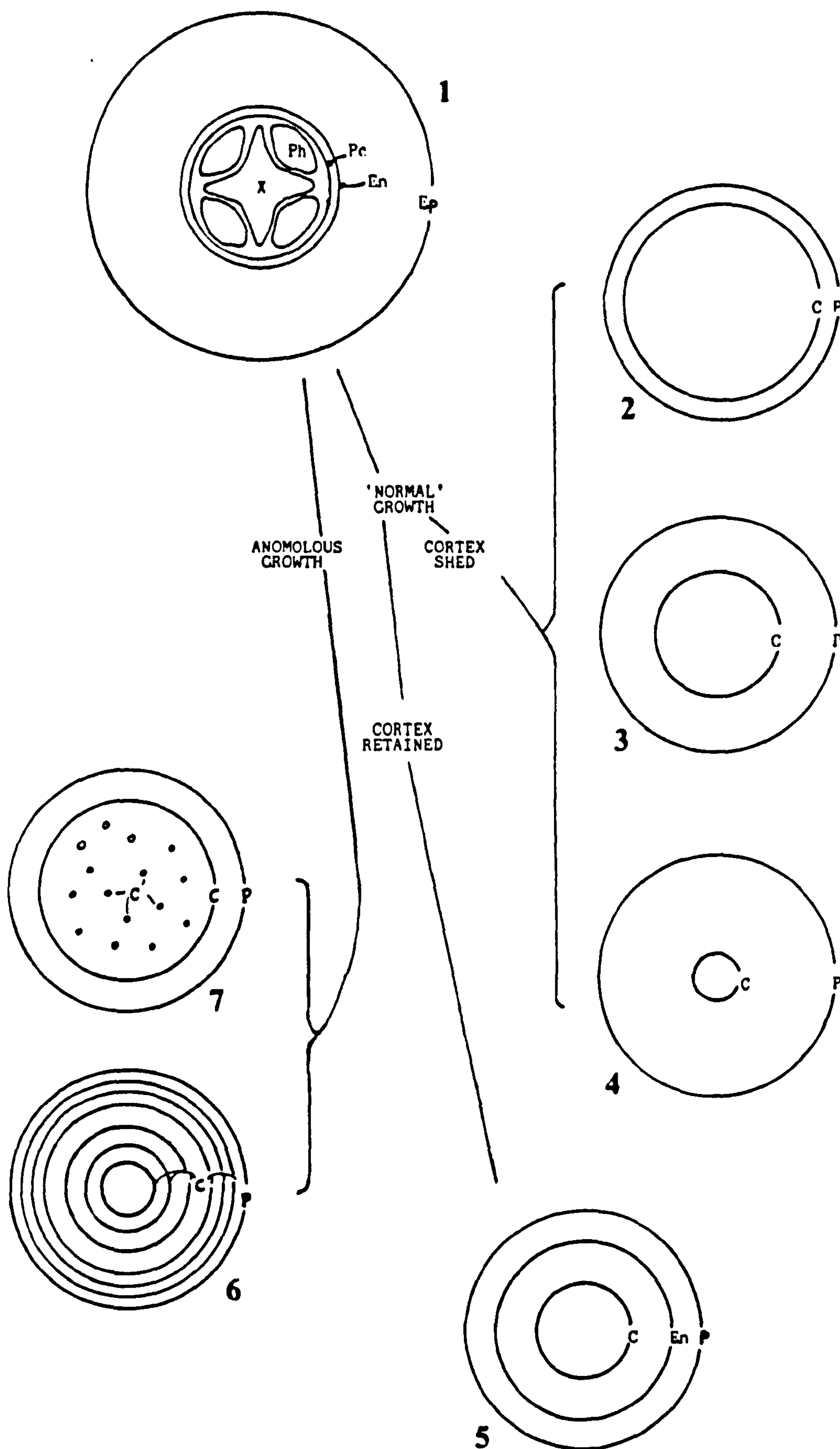


DIAGRAM 3.5 ORGANIZATION OF DICOTYLEDONOUS ROOT TISSUES
(SHOWN IN TRANSVERSE SECTION)

For the purposes of this work the arrangement of secondary tissues within fleshy roots may be divided into two groups, those with 'normal' growth and those with 'anomolous' growth. These are then further sub divided as is described below.

1) 'Normal' Growth: Here the majority of the tissues of the root are of secondary origin resulting from the division of the vascular cambium that forms between the phloem and the xylem. Both the xylem and the phloem may be largely parenchymatous. Two patterns of growth may occur.

A. Here the tissues external to the endodermis are shed during the process of secondary growth, the tissues of the endodermis and pericycle giving rise to peridermal tissue. The pericycle also divides internally to give rise to varying amounts of parenchymatous tissue. The different relative amounts of phloem and pericyclic parenchyma external to the cambium and xylem parenchyma internal to the cambium allow classification of fleshy roots with this pattern of tissue organization into three groups, though intermediates occur between them.

i) Diagram 3.5, Figure 2: development of parenchyma in the xylem far exceeds that of the phloem and the pericycle. An

example of such development is the root of Armoracia rusticana (Winton and Winton 1935).

ii) Diagram 3.5, Figure 3: development of parenchyma in the tissues of the xylem and the tissues of the phloem is equal. Such development occurs in both Daucus carota, Esau (1940), and Pastinaca sativa, Warning (1934).

iii) Diagram 3.5, Figure 4: development of parenchyma in the phloem and pericyclic tissues far exceeding that of the xylem. An example of such development is the root of Taraxacum officinale, Curtis (1940).

B. A second type of development may be seen in certain taxa where the cortex is not shed during the development of the secondary tissues. In this case three regions of parenchymatous development may be seen. A region of xylem parenchyma at the centre of the root is surrounded by the vascular parenchyma. External to this and internal to the endodermis is a region of phloem and pericyclic parenchyma. External to the endodermis are the primary tissues of the cortex. A periderm differentiates from the

epidermis or the parenchyma of the cortex. An example of this type of development may be seen in the root of Tragopogon pratensis, (Havis 1935), where the three regions of parenchymatous development are approximately equal.

2) **Anomalous Growth:** Here the process of secondary growth is limited, the majority of the tissues of the root, both parenchymatous and vascular, resulting from the division of secondary cambia, different types of such anomalous growth are presented by the taxa under study here.

A. Beta type: Anomalous secondary cambia form in concentric rings around the central primary vascular cambium. The first of these differentiates from the primary cambium, subsequent ones from the pericyclic tissues and the phloem parenchyma. The fully developed root, in transverse section, appears to have concentric cambial rings with progressively greater amounts of vascular tissue towards the centre of the root. The most central ring is the original primary cambial ring, differentiating xylem internally and phloem externally. Artschwager (1926) described this type of growth for Beta vulgaris ssp. vulgaris. This is illustrated by figure 6 of diagram 3.5.

B. Raphanus type: Subsequent to the development of the secondary tissues secondary cambia arise within the tissues of the xylem parenchyma. These form as circular zones giving rise to concentric vascular bundles and extensive amounts of parenchyma. This type of anomalous growth has been described for Raphanus raphanistrum by Hayward (1938). This is illustrated by figure 7, diagram 3.5.

C. Ipomoea type: A further anomalous growth type is that found in Ipomoea batatas. Here the secondary cambia arise around individual vessels of the secondary xylem. These give rise to phloem, xylem parenchyma and laticifers. This type of anomalous growth is not represented by any of the taxa under study here though has been described for Ipomoea batatas by Hayward (1938).

3.4 INFRASPECIFIC VARIATION

Since the identification of plants is often achieved by the recognition of the variation between diagnostic characters in different species it is always important to determine if there is variation in these diagnostic characters within the species themselves. Plant remains may be derived from a wide range of environments and exhibit a limited number of diagnostic characters.

Variation between individuals or between populations of the same species, known as infraspecific variation must be recognised if identification may proceed to the lowest hierarchical taxonomic level achievable.

Intraspecific variation may be the result of either environmental influences or genetic factors (Snaydon 1973), and in many cases it is often difficult to determine whether variation is either environmentally or genetically induced without extensive work. The margin of genetic variability may be wide or narrow depending on the liberal or conservative nature of the species boundary in question (Snaydon 1984). Environmentally induced variation is dependent on the phenotypic plasticity within the species though not all phenotypic variation is dependent on plasticity (Cook 1968). Individuals of the same species grown under uniform environmental conditions will never be phenotypically identical, observable variation being due to epigenetic effects during the expression of genes (Cook 1968). This has been termed 'developmental noise' by Waddington (1957). Heteroblastic development and maturation of tissues both cause observable variation between individuals of the same species though this is not due to phenotypic plasticity. The interaction between phenotype and genotype is great

and it is therefore difficult to determine the extent to which variation is due to plasticity.

Intraspecific variation may be expressed physiologically, anatomically, morphologically and in terms of variation in the lifecycle. Early studies such as those of Turesson (1922a, b, 1925) in Sweden and Europe and Clausen et al (1940) in America indicated the nature of intraspecific variation in terms of both genetic variability and plasticity. Studies since have explored the wide range of ways in which variation is expressed. Diagnostic characters are generally those exhibiting least plasticity, ie. with the highest predictive value.

The nature of many taxonomic studies is such that the observation of intraspecific variation is often restricted to those parts of plants that are under greatest pressure from natural selection. Variation in for example, floral characteristics is of great importance taxonomically. Variation in plant organs that are both of less taxonomic importance and less accessible to the field botanist has not been studied to the same degree.

Intraspecific variation resulting from wide genetic variability of the species is hard to differentiate from wide margins of variability resulting from phenotypic plasticity. Beta vulgaris sl., when taken to include both

sub species vulgaris and maritima is an example of how the use of wide species boundaries can create a wide margin of infraspecific variation. The root of Beta vulgaris ssp. maritima is highly ramified and relatively unswollen compared with that of Beta vulgaris ssp. vulgaris which is highly swollen and usually consists of a single unbranched axis. If Beta vulgaris L and Beta maritima L, are taken as discrete species this decreases greatly the margin of infraspecific variation within each taxon. As discrete species however, each displays a certain amount of phenotypic plasticity in itself, (Ford-Lloyd and Williams 1975).

An example of an extreme margin of variability expressed by phenotypic plasticity is that of Pastinaca sativa. Under cultivation the root is highly swollen and rarely branched. The wild form is less swollen and more often branched. Escapes from cultivation revert to the wild condition, (Simmonds 1976). Barne (1936), examining the effect of soil moisture and photoperiod on growth and carotene content of a cultivar of Daucus carota found that root shape and length were modified by temperature. For the cultivar used, average growth occurred at 60 to 70°C. Higher temperatures produced short stubby carrots whereas lower temperatures produced long thin carrots. The pattern of variability was matched to geographical regions

and their respective average temperatures across North America.

Hayden (1919), found that the swollen basal internode of Poa bulbosa when cultivated on moist soil lost its 'bulbous' nature. This led the author to believe that the swollen nature of the basal internode was a reserve of water rather than of starch or sugars. It also serves to illustrate the plastic nature of the tuberous condition of some taxa.

The morphology and anatomy of the rhizome and tuber complex of Cyperus rotundus have been observed to vary in relation to an environmental gradient, (Davis 1942, G.C. Hillman pers. comm.). The ecocline is in relation to the water content of the substrate; plants growing in relatively dry conditions form narrow rhizomes and ovoid tubers. Plants growing in waterlogged conditions form a far less heterogeneous rhizome and tuber complex with highly contorted growth. Intermediate conditions occur at intermediate moisture levels. Davis (1942), studied experimentally grown Cyperus rotundus growing in different moisture levels and found that variation in number and weight of tubers in relation to the aerial parts of the plant. An increase in soil moisture led to a significant increase in tuber biomass. Both these observations

indicate the extreme plasticity in the anatomy and morphology of this taxon. It must be noted however that although this is not an isolated case, infraspecific variation is rarely this extreme. Ayensu (1972) states, for example, that material of Dioscorea and Tamus tubers under study, 'showed a striking uniformity in their general anatomy'. This has been found to be the case with much of the tissue under examination in the present study. Most observable variation in morphology will be due to 'developmental noise' often influenced to a large extent by the physical restraints of the substrate and the maturation of the tissues.

Careful selection of characters least subject to genetic and phenotypic variation increases the possibility of making correct identifications in archaeobotanical material. This tends to narrow the range of usable characters when compared with those available for identification of present day material.

CHAPTER FOUR - MATERIALS AND METHODS

4.1 INTRODUCTION

Soft plant tissues generally undergo degrees of physical transformation on preservation, whether through charring, dessication or waterlogging. This is often in the form of expansion or shrinkage of the tissues, deterioration or loss of fragile parts and their fragmentation. This pattern of drastic changes contrasts markedly with that found in the archaeological remains of seeds and wood. Being relatively robust, the morphology of seeds and the morphology and anatomy of wood may change little on preservation (unless compressed) so that the classical morphological and anatomical criteria may be used in their identification with only minor adjustments for the effects of charring. Soft tissues, however, are rarely preserved in a state that allows identification based on direct comparisons with criteria observed in modern fresh plant material. For this reason it is necessary to undertake the experimental charring of those plants that are represented in the archaeological record by highly deteriorated and fragmented remains. The effects of heat on the anatomy and morphology of fresh tissues may be compared with those of expected archaeological tissues. Not only classical characters but also secondary

characters resulting from charring may then be used in the interpretation of similar archaeological tissues by reconstructing their probable original morphology and anatomy and thus allowing their identification by the comparison of diagnostic characters.

In this research methods have been developed for the examination of charred vegetative parenchymatous tissues. Briefly, this involves a thorough examination of the fresh morphology and anatomy of the tissues under study. Similar tissues are then experimentally charred and examined using scanning electron microscopy. A detailed series of comparisons of the morphology and anatomy of the fresh and charred tissues forms the basis of an interpretative system for use in identifying charred remains and provide the core of the thesis. Outlined below are the specific methods followed in observing modern, fresh and charred tissues and archaeological remains. Prior to this a list of materials and their sources is given.

4.2 MATERIALS

Presented below are three tables outlining the plant materials, archaeological samples and other materials used in this research. Alongside each are given the sources of

the materials. The order followed here is retained in the second and third chapters of results.

4.2.1 Vegetative Plant Tissues

The taxa bearing roots, tubers and rhizomes etc. used in this research are listed below. These are arranged alphabetically under systematically ordered family headings. This arrangement follows that of Stebbins (1974).

The basis for the selection of each of the taxa examined has been outlined in the introduction to the thesis. While the selection reflected very much the aims of the project it had no influence on the overall methodology.

The materials listed below were obtained from a number of different sources. In every case an attempt was made to obtain fresh material. In some cases however this was not possible, and dried material from collections at the Royal Botanic Gardens at Kew was used. Due to the need to conserve these collections it was not possible to use very much material in these cases.

Sufficient fresh material was observed to ensure that the occurrence of any infraspecific variation could be

TABLE 4.1 VEGETATIVE PLANT TISSUES

TAXA	SOURCE
HYPOLEPIDACEAE	
<u>Pteridium aquilinum</u> (L) Kuhn	Fresh Material : British.
ASPIDIACEAE	
<u>Dryopteris filix-mas</u> (L) Schott	Fresh Material : British.
POLYPODIACEAE	
<u>Polypodium interjectum</u> Shivas	Fresh Material : British.
NYMPHAEACEAE	
<u>Nuphar advena</u> Ait.	Fresh Material : Commercial (Hort.)
<u>Nymphaea alba</u> L.	Fresh Material : Commercial (Hort.)
RANUNCULACEAE	
<u>Anemone nemorosa</u> L.	Fresh Material : British
<u>Ranunculus ficaria</u> L.	Fresh Material : British
CARYOPHYLLACEAE	
<u>Cypsophila struthium</u> L.	Dried Material : RBG Kew (Egypt)
CHENOPODIACEAE	
<u>Beta vulgaris</u> ssp <u>maritima</u> (L) Arcangeli	Fresh Material : British
<u>Beta vulgaris</u> ssp <u>vulgaris</u> (= <u>B. Vulgaris</u> (L))	Fresh Material : Commercial (Food)
POLYGONACEAE	
<u>Polygonum bistorta</u> L.	Dried Material : RBG Kew (Britain).
<u>Rheum palaestinum</u> Feinbr.	Fresh Material : Jordan
<u>Rheum rhaponticum</u> (L)	Fresh Material : Commercial (Hort.)
CUCURBITACEAE	
<u>Bryonia dioica</u> Jacq.	Fresh Material : British
CRUCIFERAE	
<u>Armoracia rusticana</u> P Gaertner, B Meyer & Scherb.	Fresh Material : British.
<u>Brassica campestris</u> ssp <u>rapifera</u>	Fresh Material : Commercial (Food)

TAXA	SOURCE
<p>CRUCIFERAE (Cont.)</p> <p><u>Crambe cordifolia</u> Stev.</p> <p><u>Crambe maritima</u> L.</p> <p><u>Raphanus sativus</u> ssp <u>radiculata</u> (= <u>R. sativus</u> L.)</p> <p>PRIMULACEAE</p> <p><u>Cyclamen persicum</u> Mill.</p> <p>ROSACEAE</p> <p><u>Potentilla anserina</u> L.</p> <p>LEGUMINOSAE</p> <p><u>Lathyrus linifolius</u> (Reichard) Bassler (= <u>L. montanus</u> Bernh.)</p> <p>ONAGRACEAE</p> <p><u>Oenothera biennis</u> L.</p> <p>GERANIACEAE</p> <p><u>Biebersteinia multifida</u> D.C.</p> <p><u>Erodium glaucophyllum</u> (L) L'Her</p> <p>UMBELLIFERAE</p> <p><u>Conopodium majus</u> (Gouan) Coret</p> <p><u>Daucus carota</u> ssp <u>sativus</u> (Hoffm.) Areangeli</p> <p><u>Eryngium maritimum</u> L.</p> <p><u>Heracleum sphondylium</u> L.</p> <p><u>Myrrhis odorata</u> L.</p> <p><u>Pastinaca sativa</u> L.</p> <p>GENTIANACEAE</p> <p><u>Gentiana lutea</u> L.</p> <p>SOLANACEAE</p> <p><u>Withania somnifera</u> Dunal.</p> <p>BORAGINACEAE</p> <p><u>Lithospermum erythrorhizon</u> Sieb. & Zucc.</p>	<p>Dried Material : RBC Kew (Afghanistan)</p> <p>Fresh Material : British</p> <p>Fresh Material : Commercial (Food)</p> <p>Fresh Material : Jordan</p> <p>Fresh Material : British</p> <p>Fresh Material : British.</p> <p>Fresh Material : British</p> <p>Fresh Material : Jordan.</p> <p>Fresh Material : Jordan.</p> <p>Fresh Material : British</p> <p>Fresh Material : Commercial (Food)</p> <p>Fresh Material : British</p> <p>Fresh Material : British</p> <p>Fresh Material : British</p> <p>Fresh Material : British</p> <p>Dried Material : RBC Kew (France).</p> <p>Dried Material : RBC Kew (India)</p> <p>Dried Material : RBC Kew (Europe)</p>

TAXA	SOURCE
BORAGINACEAE (Cont.)	
<u>Symphytum officinale</u> L.	Fresh Material : British
OROBANCHEACEAE	
<u>Cistanche tubulosa</u> Shenk (Wight)	Fresh Material : Jordan
COMPOSITAE	
<u>Anacyclus pyrethrum</u> D.C.	Dried Material : RBC Kew (Europe)
<u>Arctium minus</u> Bernh. <u>sl</u>	Fresh Material : British
<u>Cichorium intybus</u> L.	Fresh Material : British.
<u>Doronicum grandiflorum</u> Lam	Dried Material : RBC Kew (Jordan)
<u>Inula helinium</u> L.	Dried Material : RBC Kew (Europe)
<u>Saussurea lappa</u> C.B. Clarke	Dried Material : RBC Kew (Europe)
<u>Scorzonera hispanica</u> L.	Fresh Material : Commercial (Food)
<u>Scorzonera judaica</u> Eig.	Fresh Material : Jordan.
<u>Scorzonera schweinfurthii</u> Boiss	Fresh Material : Jordan.
<u>Taraxacum officinale</u> <u>sl</u>	Fresh Material : British.
<u>Tragopogon pratensis</u> L.	Fresh Material : British
BUTOMACEAE	
<u>Butomus umbellatus</u> L.	Alcohol preserved Material: RBC Kew (british)
ALISMATACEAE	
<u>Alisma lanceolatum</u> With.	Fresh Material : British
<u>Alisma plantago-aquatica</u> L.	Fresh Material : British
<u>Sagittaria sagittifolia</u> L.	Fresh Material : British
GRAMINEAE	
<u>Arrhenatherum elatius</u> ssp <u>bulbosum</u> (Willd.) Hyl.	Fresh Material : British
<u>Hordeum bulbosum</u> L.	Fresh Material : Jordan
CYPERACEAE	
<u>Cyperus esculentus</u> L.	Fresh Material : Commercial (Food)
<u>Cyperus longus</u> L.	Dried Material : RBC Kew (Egypt)
<u>Cyperus rotundus</u> L.	Fresh Material : Egypt.
<u>Schoenoplectus tabernaemontani</u> (C.C.Gmelin) Palla	Fresh Material : British
<u>Scirpus maritimus</u> L.	Fresh Material : British.

TAXA	SOURCE
TYPHACEAE	
<u>Typha angustifolia</u> L.	Fresh Material : British
<u>Typha latifolia</u> L.	Fresh Material : British
SPARGANIACEAE	
<u>Sparganium erectum</u> L.	Fresh Material : British
ZINGIBERACEAE	
<u>Alpinia galanga</u> Sw.	Fresh Material : Commercial (Food)
<u>Curcuma domestica</u> Valet.	Fresh Material : Commercial (Food)
<u>Zingiber officinale</u> Rosc.	Fresh Material : Commercial (Food)
ARACEAE	
<u>Acorus calamus</u> L.	Dried Material : RBG Kew (British)
<u>Arum maculatum</u> L.	Fresh Material : British
IRIDACEAE	
<u>Crocus sativus</u> L.	Fresh Material : Commercial (Hort.)
LILIACEAE	
<u>Asphodelus aestivus</u> Brot.	Fresh Material : Jordan
<u>Polygonatum X hybridum</u> Brugger	Fresh Material : Commercial (Hort.)
DIOSCOREACEAE	
<u>Tamus communis</u> L.	Fresh Material : British
ORCHIDACEAE	
<u>Orchis mascula</u> (L) L.	Fresh Material : British

TAXA	SOURCE
TYPHACEAE	
<u>Typha angustifolia</u> L.	Fresh Material : British
<u>Typha latifolia</u> L.	Fresh Material : British
SPARGANIACEAE	
<u>Sparganium erectum</u> L.	Fresh Material : British
ZINGIBERACEAE	
<u>Alpinia galanga</u> Sw.	Fresh Material : Commercial (Food)
<u>Curcuma domestica</u> Valet.	Fresh Material : Commercial (Food)
<u>Zingiber officinale</u> Rosc.	Fresh Material : Commercial (Food)
ARACEAE	
<u>Acorus calamus</u> L.	Dried Material : RBG Kew (British)
<u>Arum maculatum</u> L.	Fresh Material : British
IRIDACEAE	
<u>Crocus sativus</u> L.	Fresh Material : Commercial (Hort.)
LILIACEAE	
<u>Asphodelus aestivus</u> Brot.	Fresh Material : Jordan
<u>Polygonatum X hybridum</u> Brugger	Fresh Material : Commercial (Hort.)
DIOSCOREACEAE	
<u>Tamus communis</u> L.	Fresh Material : British
ORCHIDACEAE	
<u>Orchis mascula</u> (L) L.	Fresh Material : British

determined. Where possible, individuals of the same taxa were examined from different populations as well as individuals at different stages of maturity from the same population. Fresh material was collected from both Britain and Jordan. In both countries plants were collected from sites where no damage would be done to wild populations.

Material was collected in Jordan over a one month period of field work during March and April 1987, funded by the Science and Engineering Research Council. This played an important part in the research project since it made available taxa which extended the scope of the research.

Two sources of commercially available plant material were used: those sold as food and those sold as horticultural plants. Taxa in these categories are indicated.

4.2.2 Additional Materials

Listed below are the additional materials that were examined for comparison with those listed in table 4.1. These are listed in the same order as in the illustration section and are described in Chapter five. All are modern with the exception of the archaeological remains of Hordeum vulgare and Secale cereale.

TABLE 4.2 ADDITIONAL MATERIALS

TAXA	SOURCE
FAGACEAE	
<u>Quercus robur</u> L.	
fruit	Fresh Material: British
gall	Fresh Material: British
POLYGONACEAE	
<u>Rheum rhaponticum</u> L.	
petiole	Fresh Material: Commercial (Food)
MORACEAE	
<u>Ficus carica</u> L.	
fruit	Fresh Material: Commercial (Food)
ROSACEAE	
<u>Malus domestica</u> L.	
fruit	Fresh Material: Commercial (Food)
UMBELLIFERAE	
<u>Apium graveolens</u> L.	
petiole	Fresh Material: Commercial (Food)
<u>Heracleum sphondylium</u> L.	
petiole	Fresh Material: Commercial (Food)
GRAMINEAE	
<u>Hordeum vulgare</u> L.	
grain	Archaeological Material: Stafford, St. Marys (ST 29) Anglo Saxon
<u>Secale cereale</u> L.	
grain	Archaeological Material: Stafford, St. Marys (ST 29) Anglo Saxon
DUNG	
Donkey	Jordan
Goat	Jordan

4.2.3 Archaeological Materials

Listed here are the three groups of archaeological remains that have been examined. The sources of these remains are indicated and further details are given in Chapter seven.

TABLE 4.3 ARCHAEOLOGICAL REMAINS

TAXA	SOURCE
<p>AQABA REMAINS</p> <p><u>Sparganium</u> sp</p>	<p>Aqaba Town Remains : Jordan : Early Islamic</p>
<p>STONEHENGE REMAINS</p> <p>Indet. Root Tuber</p>	<p>Stonehenge Environs Project: Trust for Wessex Archaeology: Neolithic.</p>
<p>WADI KUBBANIYA REMAINS</p> <p><u>Cyperus rotundus</u> L.</p>	<p>Wadi Kubbaniya: Upper Egypt: Late Palaeolithic</p>

4.3 METHODS

4.3.1 Examination of Fresh Material

The method of using modern experimentally charred material of known taxa to identify unknown archaeological material poses fewer problems if charring has changed the appearance of the tissues only slightly. When, as is the case with much of the parenchymatous tissue under study here, charring causes so much destruction and deterioration that individual tissues may be unrecognisable modern fresh plant material has to be used to interpret the charred tissues.

The modern uncharred organs were examined for all taxa. Morphology was observed using the naked eye and low power reflected light microscopy. Anatomy was examined using transmitted light microscopy of stained thin sections.

Sections between twenty and one hundred microns thick were taken using a Reichart Jung sledge microtome, the thickness of the sections depending on the nature of the tissues. Those made up of relatively small parenchymatous cells could be sectioned thinner than those made up of larger cells. Difficulty in sectioning, leading to the disintegration of the sectioned tissues occurred with many

organs. This was often due to combinations of structural and parenchymatous tissues or aerenchymatous and parenchymatous tissues in close proximity. This was overcome by taking a combination of both large thick sections and much smaller thin sections and by sectioning separately different tissues of the same organ. Together these techniques were adequate to allow a full understanding of the organ.

Depending on the nature of each organ radial and longitudinal sections were taken as well as transverse sections. In a few cases oblique sections were also taken.

Before staining, some sections were cleared using a strong commercially available bleach. This removed all cell contents apart from calcium oxalate crystals leaving only the cell walls to be stained. In other sections cell contents were left intact. The staining procedure was as follows:-

1. 4% Aqueous solution of Alcian Blue for 1 to 3 minutes.
2. Wash in water for 1 to 3 minutes with occasional agitation.
3. 1% solution of Safrinin in 30% alcohol for 1 to 3 minutes.

4. Wash in 50% alcohol for 3 to 15 minutes.
5. 70% alcohol for 5 minutes.
6. 95% alcohol for 5 minutes.
7. 100% alcohol for 5 minutes.

The time allowed for each step was modified depending on the thickness and composition of certain sections. The method is that developed at the Anatomy department of the Jodrell Laboratory of the Royal Botanic Gardens at Kew.

The sections were mounted onto glass slides in 'Euparal' mountant and dried for 6 to 8 weeks at 45°C.

For some taxa fresh material was not available for sectioning and so modern dried tissue was used. This had to be boiled in water for approximately 20 minutes for them to be soft enough to section. On boiling any loss of size due to drying was fully recovered.

The mounted sections were examined using a 'Wild 8' transmitted light microscope. This had x10 eyepieces and x2, x10, x25 x40 and x100 objectives giving a wide range of magnification.

4.3.2 Experimental Simulation of Charred Archaeological Plant Remains

The experimental charring of plant material to simulate archaeological plant remains has previously been undertaken by archaeobotanists for both seeds and wood. Hopf (1955) investigating the effect of charring on seeds of Triticum and Hordeum species used a temperature of 220°C and a charring period of 4 to 6 hours. Prior and Alvin (1983), working on wood used a range of temperatures, charring for a one hour period. Wilson (1983) used both a range of temperatures and charring periods experimenting on weed seeds. There is no record of experimental charring on parenchymatous tissues and so the charring regime used here has been based on experimental results rather than previously published work.

Charring was carried out using a 'Gallenkamp' muffle furnace with a temperature range of 100 to 1000°C. To obtain a pattern of charring close to that observable in archaeological charcoals a number of variables were considered:-

- 1.. Temperature
- 2.. Charring Period
- 3.. Charring Substrate

4. State of Tissue, a) Pre-dried or fresh (wet)
b) Size of organ or tissue
fragment

The Temperature and Charring period are linked to a certain extent. A lower temperature with a longer charring period may have the same results as a higher temperature with a shorter charring period. The two are however, independant to some extent in that low temperatures will not cause charring however long the charring period, and high temperatures will cause ashing however short the charring period.

Temperatures of between 200 and 500°C cause the charring of modern plant material in a manner comparable with charred archaeological remains, with charring period between being between 2.5 hours and 4 hours depending on the state of the tissue. Electron Spin Resonance (ESR) studies of archaeological plant remains have generally indicated a highest past temperature of between 220 and 300°C (Hillman et al, 1985). Since it is easier for either the temperature or charring period to remain fixed and the other to vary depending on the state of the tissue, the parameters chosen were a temperature of 250°C and a charring period of between 2.5 and 4 hours. The smaller and drier the fragments of tissue or organ the

shorter the charring period required to achieve a state similar to that observed in archaeological remains.

In a typical domestic fire, charcoal is generally formed in the reducing conditions of the ash at the base of the fire rather than in the oxidising conditions of the open flame which will eventually reduce most tissue to ash. Small dense fragments of tissue will fall through the structure of the fire into the ash and therefore survive. Larger fragments tend to lodge in the structure of the fire and partially or totally turn to ash. Any small fragments surviving this process will fall through the fire. For this reason, the experimental simulation of archaeological charcoal was carried out with the fragments buried in a substrate, rather than charred in air. This simulates the reducing conditions at the base of the fire. Sand has been used in comparable experimental simulations (Prior and Alvin 1983), but here wood ash was chosen to represent as closely as possible the archaeological conditions of charring. The ash was homogeneous and able to pass through a 200 μm sieve, allowing easy retrieval of the charred plant material by sieving.

The charring regime incorporated a range of states of the tissue under study; whether the organ is whole or fragmented, large or small and dried and fresh (wet).

Thus all the taxa under observation were charred in a fresh (wet) state and after a period of drying. The drying was carried out in a 'Gallenkamp' drying oven at 100°C for between 24 and 96 hours, depending on the size of the organ or tissue fragment. Ranges of fragment sizes were charred for larger organs. Organs measuring 3 to 4 cm across or less were charred whole.

4.3.3 Observation of Charcoal

Each of the techniques available for the observation of charcoal pose their own problem as well as advantages over the other methods. For magnification of between x6 and x50 a low power reflected light microscope was used. For high power observation three methods were available: thin sections for transmitted light microscopy, epi-illuminated light microscopy and scanning electron microscopy. Thin sections may be ground for transmitted light microscopy, but while this gives a direct comparison with thin sections of fresh material it is a lengthy and destructive method. Epi-illuminated light microscopy and scanning electron microscopy are similar in that a surface of an opaque specimen may be observed in detail. The former has the advantage of being simple and quick; scanning electron microscopy, though by no means complicated does require preparation and is a more lengthy process but does offer a

greater depth of field than epi-illuminated light microscopy. This is important considering that a flat fracture plane is difficult to achieve in much of the charred parenchymatous tissues. Higher magnifications are possible while maintaining good resolution. Manoeuvrability of the specimen also allows for more information to be gained from each fragment of charcoal.

Taking into account the above considerations it was decided that scanning electron microscopy should form the major method of examination used in this research.

The instrument used here was the JEOL T100 SEM. This met the basic requirements for observation of this type of material, good resolution up to x3500 at low accelerating voltages. Good manoeuvrability of the stage was also available.

Fragments of charred tissue up to 1 cm across and 1 cm high were mounted on 'Cambridge' type electron microscope stubs. Fast drying glues, double sided tape, LEIT-C a conductive carbon cement and LEIT-C Plast, a conductive plasticine-like material were used as mountants, depending on the nature of the specimen. Larger harder specimens required a glue to hold the specimen in place whereas small fragile fragments required a less damaging mountant

such as double sided tape, conductive cement or LEIT-C Plast. Specimens that needed to be removed from the stub following microscopy were mounted with LEIT-C Plast. If the mountant used was non-conductive then a conductive contact was made between the specimen and the stub using thinned down conductive cement. All specimens were sputter coated with gold using an Edwards S 105 B sputter coater. At a setting of 1.2 Kv, 20 mA and 2 bars pressure at a working distance of 30 mm, a coating of approximately 0.23 nm per second was achieved. Specimens were coated for 1.5 minutes giving a relatively thick coat. This was necessary for both allowing the gold to permeate the many crevices in the charcoal and to help hold the fragile charcoal together during electron microscopy.

The results of the electron microscopy study are illustrated by a series of scanning electron micrographs. These were taken in Ilford FP4 220 film using a Mamiya camera adapted for use on the microscope. All photographs were taken at an accelerating voltage of 15 Kv.

4.3.4 Archaeological Charcoal

The three samples of archaeological charcoal were observed using both low power reflected light microscopy and scanning electron microscopy. Specimens were mounted

using LEIT-C Plast referred to above to allow their removal following microscopy.

4.4 EXPLANATION OF TERMS

Some terms used in this thesis that may be slightly ambiguous in nature and require some explanation if their definition and use here is to be fully understood.

The word 'charcoal' is often understood as being specifically charred wood, the tissue of the secondary xylem in many perennial plants. Here however the term is extended to cover fragments of other charred plant tissues especially where the organ of origin is unknown. The term 'charcoal' is therefore used to cover charred soft tissues of vegetative and non-vegetative origin as well as wood.

Charcoal is produced by the reduction of plant (or other) tissue to elemental carbon. The remains of charred plant tissues however contain many impurities as well as elemental carbon. This is evident from the need to sputter coat specimens prior to scanning electron microscopy. For simplicity though, in this thesis the substance that charcoal is composed of is termed 'carbon'.

All botanical terms that are not explained in the text are defined by most botanical dictionaries such as Jackson (1928) and Tootill (1984).

CHAPTER FIVE - RESULTS 1 - THE ANATOMY OF CHARRED
VEGETATIVE PARENCHYMATOUS TISSUES

5.1 INTRODUCTION

It is necessary to give a general review of the characters of charred vegetative parenchymatous tissue, with specific examples, before individual descriptions of species are given. Morphology and anatomy of such charred tissue may then be interpreted before an identification is attempted. Those characters of important diagnostic value will be indicated. Equal weight will be given to characters common to all or most taxa that are important in the interpretation of the morphology and the anatomy, although they may be of little diagnostic value.

In part, classical anatomical and morphological characters are indicated as methods for identification and description. However since much tissue is deteriorated or undergoes alteration it is necessary to reappraise the classical methods in order to describe artifactual characters of the tissue.

It is also necessary to recognise how different conditions and states of plant material may lead to different results in the charring process. These may be summarised as

follows:

- 1) Varying patterns of preservation and deterioration due to differences in gross morphology and tissue organisation.
- 2) Different sizes of organ and tissue fragment.
- 3) Varying water contents on charring leading to different states of deterioration.
- 4) Differences resulting from fracturing before and after charring.

5.2 GROSS MORPHOLOGY

While organs, larger fragments of organs and less frequently small fragments of larger organs often have the remains of the original external surface, these rarely possess the microscopic characters useful in identification. Fragments of external surface, if large enough, may permit an interpretation of their external

morphology which could lead to an identification. Macroscopic characters such as nodes, scars left by the detachment of rhizomes, stolons, roots, scale leaves, buds, petioles and other aerial parts are of diagnostic value. Since the detachment of many of these organs leave scars that contain a concentration of vascular and mechanical tissues, especially xylem, they may survive the process of charring and subsequent taphonomic processes. Occasionally these features survive where the external surface does not leave the vascular tracts of the detached organ protruding from the body of the fragment.

Where the whole organ is preserved intact identification may be possible from the gross morphology alone. Intact preservation of a whole organ is more common for small storage organs such as occur in Cyperus rotundus, Anemone nemorosa or Lathyrus linifolius rather than for larger organs such as the tuber of Tamus communis or the roots of Beta vulgaris, Oenothera biennis or Myrrhis odorata.

Surface features of some organs may be helpful in identification of or at least in distinguishing between otherwise similar species. Examples are the wrinkled surface of Daucus carota and Polygonum bistorta which may be distinguished from the smooth surface of Beta vulgaris or Taraxacum officinale.

5.3 SURFACES OF CHARRED FRAGMENTS

A fragment of charred tissue may contain any of three types of external surface summarised in Table 5.1 below. As previously stated the charred remains of original

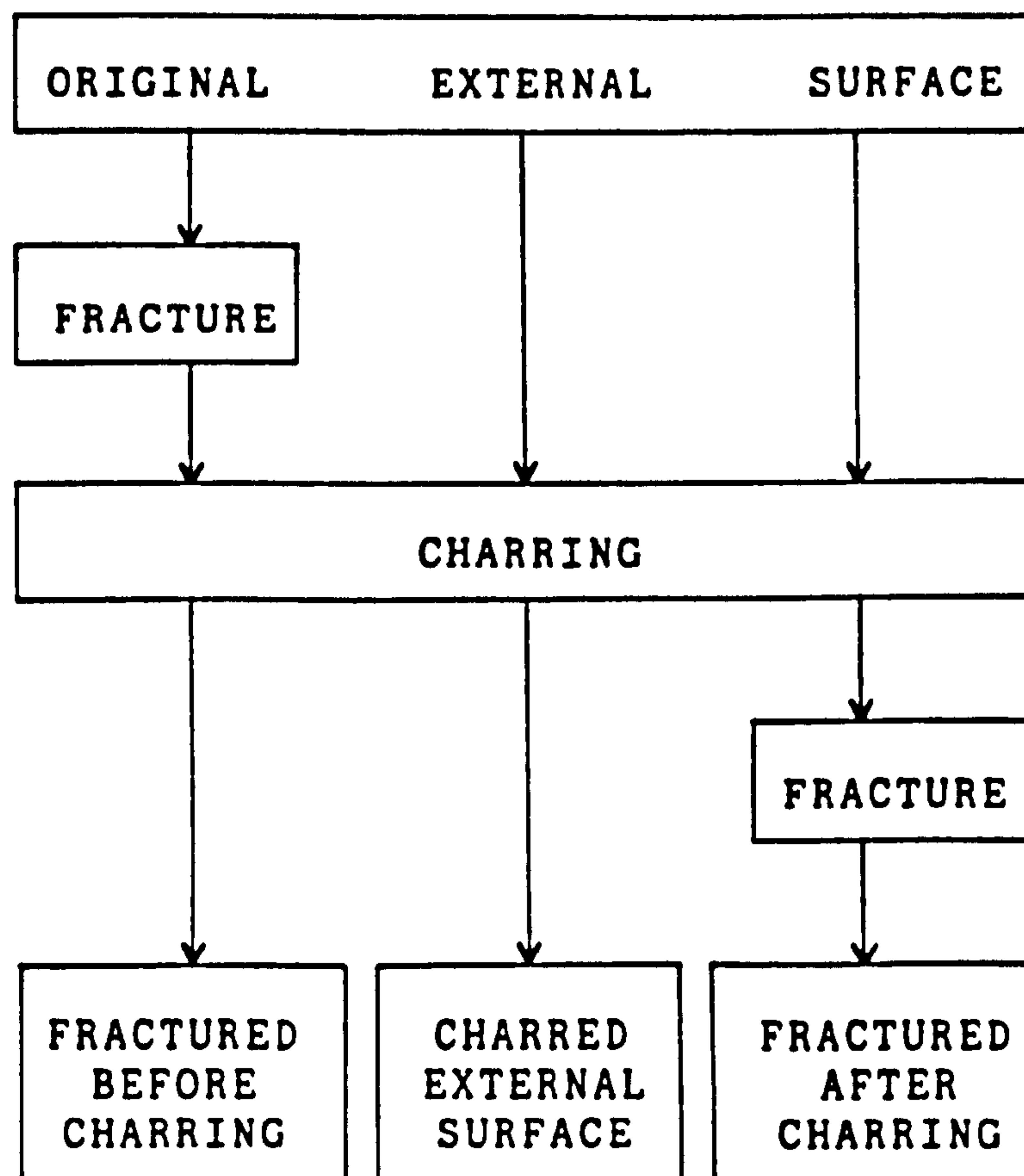


TABLE 5.1 THE ORIGIN OF SURFACES ON A FRAGMENT OF CHARRED TISSUE

external surface, epidermis or periderm, may survive.

Prior to charring however the surface may have been broken by a fracture more or less perpendicular to the surface or by removal of the tissues parallel to the surface. On charring this will produce a derived surface of exposed internal tissues. The heat received by the surface will be greater than that by the tissues within the fragment; factors such as tension and pressure within the tissues will be different from those on the surface of the fragment and high temperatures will cause ashing of the external surface and the deterioration of the tissue below it. A derived surface caused by a fracture after the process of charring will differ from this since it has not been subjected directly to such high temperatures. This is illustrated well by a transverse section through the tissues fractured after charring, as shown in Fig 9, Plate 8 and Figs 1 to 4 on Plate 9, of Beta vulgaris ssp. maritima. The transverse section of charred tissue fractured prior to charring is seen in Figs 7 and 8 on Plate 8. The parenchyma between the rings of vascular tissue in the fragments fractured prior to charring have deteriorated leaving concentric cavities. In those fractured after the process of charring the parenchyma has become vesicular.

A whole, large organ such as Tamus communis, fractured prior to charring will result in charred remains quite

different from a whole tuber of the same species fractured after charring. Small fragments of a larger organ when charred will contain surfaces that have mostly been in contact directly with intense heat. Small fragments of a larger organ, fractured after charring will mostly contain surfaces that have not been in contact directly with intense heat. Differentiation between the two types of surface will depend on the charring conditions and the particular species involved. These observations apply more to larger organs than to smaller ones, such as the tuber of Cyperus rotundus, which will on the whole react as the tissue of a larger organ fractured prior to charring. Exceptions will also occur.

Any characters useful in identification surviving on any surface of a fragment, whether the surface has resulted from a fracture before or after charring, or if the surface is of epidermis or periderm tissue, are likely to be obliterated by erosion and weathering of the charcoal. The attachment to the surfaces of the fragment of debris, before, during, or after the process of charring may also obscure diagnostic features.

5.4 CAVITIES IN CHARRED TISSUE

Sections through most fragments of charred parenchyma often reveal cavities within the tissue. The cavities may be regular, irregular, random or in a set pattern with either broken walls or smooth internal surfaces. The appearance of these cavities and their mode of origin is related to the type of organ and their position within it. There are several different types of cavity, described below, each having a different origin and structure. Only in some cases are they of diagnostic importance.

5.4.1 Vesicles and Tension Fractures

Both vesicles and tension fractures can form in the same tissue of a number of organs. In some tissues only vesicles will form when the tensions and pressures that cause fractures are absent. Some vesicles may originate partly from tension fractures, many cavities are due to a combination of both stress and vesicle formation.

Vesicular cavities are formed by the expansion of water vapour within the tissues during heating. The internal surface of the vesicle becomes, by compression, smooth but has the impression of cell outlines upon it. Cell boundaries are characterised by ridges and cell lumina by

depressions. Tension fractures are formed when the stress between the tissues caused by the shrinkage of the organ due to water loss, tears cells apart. Such fractures are characterised by internal surfaces that are composed of broken cells and cell wall debris. Different types of organ may be characterised by having both vesicles and tension fractures in different positions. Both tension fractures and vesicles occur more frequently and are larger in tissues charred from the fresh state than in those that have been dried prior to charring. This is due to water loss being greater, and therefore vesicle formation and tissue destruction being greater in fresh rather than dried tissues. This is the case with a great many of the taxa under observation.

In many charred 'tap roots' separate areas are apparent: an outer region external to the cambium and an internal region below the cambium. The roots of different species vary in structure and one of these regions may be larger than the other. In transverse section tension fractures and vesicles in the outer region have their long axis tangentially (periclinally) orientated. They may be only a few cells wide or they may spread across the entire circumference of the root. Such fractures are common between the outer and inner regions of the root along the line of the cambium.

When vesicles or tension fractures occur internally to the cambium they often radiate out from the central long axis of the root. On compression and charring the parenchyma between the cavities is often reduced to solid carbon. Examples of this type of preservation are found in the charred roots of Taraxacum officinale (Fig. 1, Plate 39) and Daucus carota (Fig. 10, Plate 22 and Figs. 1,4, Plate 23).

Cavities of the same type occur in organs other than the fleshy secondary roots described above. In small more or less spherical root tubers such as Lathyrus linifolius (Figs. 5 to 8, Plate 9) and Conopodium majus (Fig. 7, Plate 22) tangentially orientated fractures and vesicles occur in the outermost tissues and additional cavities radiate out from a central point within the tuber. In larger, more irregularly shaped tubers such as Arum maculatum (Fig.9, Plate 54) and Sagittaria sagittifolia (Figs. 4 and 5, Plate 42), both vesicles and tension fractures occur but their positions are far more random. Vesicles occur either as more or less spherical cavities or as very irregular cavities with internal surfaces consisting of well preserved non-compressed cell layers. The tissues between the vesicles or between vesicle and the external surface of the organ or fragment may or may not be compressed.

In rhizomes similar vesicles may occur; these are randomly placed but always have their long axis parallel to that of the rhizome. They are usually more or less circular in transverse section. Again the internal walls may be made up of compressed or non-compressed cell remains. Examples of this type of preservation are found in the charred rhizomes of Anemone nemorosa (Fig. 4, Plate 6).

Vesicles and tension fractures occur in many charred parenchymatous tissues and so are rarely diagnostic though they are useful in determining the nature and size of the organ from which a small fragment has originated. The extent to which vesicles and tension fractures occur may indicate the water content of the organ on charring.

5.4.2 Secretory cavities

Secretory cavities occur in the tissues of some members of the Compositae and are in appearance similar to vesicles. The epithelial cells become compressed and solidified giving the impression of a thicker compressed layer of tissue. The tissue containing such cavities is often well preserved and not often associated with very vesicular charcoal. Tension fractures however do often occur in the same tissue. Secretory cavities are found in the charred tissues of the fleshy secondary roots of Anacyclus

pyrethrum (Figs. 1 to 3, Plate 32), Inula helenium (Fig. 8, Plate 35) and Saussurea lappa (Figs. 3 to 5, Plate 36) and may be of some diagnostic value.

5.4.3 Tissue deterioration

Cavities in a tissue caused by actual destruction of cells are not common in a tissue composed entirely of parenchyma, but are more common in the vascular tissues, particularly in the phloem. The primary pentarch stele in the root tubers of Ranunculus ficaria (Fig. 8, Plate 6), often deteriorates completely leaving a central fissure or cavity. The phloem in the individual bundles of Scirpus maritimus also deteriorates to leave a cavity, (Fig. 8, Plate 48). Whereas phloem commonly deteriorates it is less common to find destruction of the whole vascular tract; more often than not some elements of the xylem will remain intact.

5.4.4 Small vesicles

In some cases charring causes the loss of cell wall structure with some collapse and fusion of the tissues resulting in the formation of a carbon matrix containing numerous small vesicles. These represent some of the former cell lumina and intercellular air spaces. The

distance between the vesicles is varied but it is important to note that the charred tissue contains a greater proportion of carbon to vesicle. An example of this type of charcoal is found in the charred parenchymatous tissues of Arum maculatum (Fig.1, Plate 55). An isolated fragment of this type of charcoal is unlikely to be identifiable by its anatomy.

If there is little fusion of the cell walls a similar type of charred tissue forms which is composed entirely of thick walled vesicles rather than solid carbon containing well spaced vesicles. This type of charcoal is typified by the charred outer tissues of the fleshy secondary root of Scorzonera hispanica (Fig. 1, Plate 37).

5.4.5 Natural Breakdown Cavities

Cavities formed by the breakdown of tissues occur naturally in some organs which, when charred, appear as breakdown cavities formed as a result of charring. The most common occurrence of this type is in the central pith of some stem structures. Examples are found in the stolon of Doronicum grandiflorum (Fig. 7, Plate 34, and Fig. 1, Plate 35) and Arrhenatherum elatius ssp. bulbosum (Fig.9, Plate 42).

Cavities of one type or another form in most parenchymatous tissues and their interpretation as artifact, tissue breakdown or anatomical structure is important if an identification is to be reached.

5.5 WATER CONTENT OF TISSUES PRIOR TO CHARRING

The water content of a fleshy organ prior to charring often determines the extent to which the tissue will be altered or damaged and the form in which these occur. In tissues that normally form vesicles on charring, charring from a fresh (wet) condition produces more vesicles than if charred from a dried condition. A fragment of tissue that has been dried for a long period prior to being charred and so contains a minimum water content often results in a charcoal with few vesicles and extremely good preservation. This phenomenon may be seen in the root tubers of Ranunculus ficaria and Asphodelus aestivus and the fleshy secondary root of Daucus carota. In Ranunculus ficaria a charred fresh tuber will become 'hollowed out' by either one or a small number of large vesicles compressing all the tissues against the internal surface of the outermost tissues (Figs. 8 to 10, Plate 7). If dried prior to charring then most of the internal tissues are preserved intact (Figs. 7 and 8, Plate 6). In both Asphodelus aestivus and Daucus carota the characteristic

cavities radiating out from the central long axis of the root are fewer and smaller in tissues that have been dried prior to charring. Compare, for Asphodelus aestivus, Fig. 7, Plate 56 (dried) with Fig. 3, Plate 57 (fresh). For Daucus carota, compare Fig. 2, Plate 23 (dried) and Fig. 5, Plate 23 (fresh).

The more water an organ contains at the time of charring the more frequent and larger the vesicles will be because it is by the expansion of water vapour in the tissues that vesicles are formed.

Another effect of drying parenchymatous tissue prior to charring is illustrated by the rhizome of Anemone nemorosa. Here, in charred fresh tissue the cell boundaries are clearly visible but the cells themselves are composed of solid carbon. No discrete cell contents are visible, (Figs. 4 to 5, Plate 6). In tissues that have been dried prior to charring the cell boundaries are still visible but the cells are seen to be packed with individually discernable starch grains, (Fig. 4, Plate 16). These are preserved well at the centre of the rhizome, but towards the outer tissues, the individual starch grains become less discernable as they become fused with each other, (Fig. 9, Plate 5). In the outermost cells the starch grains are fused completely leaving the

cells solid as in tissue that has been charred from the fresh state, (Fig. 8, Plate 5).

The outer tissues of a dried rhizome char in a similar manner to the tissues throughout a rhizome charred from the fresh state. It is possible that the intense heat throughout a charring fresh (wet) rhizome and in the outer tissues of a dried rhizome cause the starch grains within the cells to fuse. A slower rise to a less intense heat at the centre of rhizomes dried prior to charring allows the cell contents to be preserved intact.

Similar charcoal results from the charring of tissues of the tuber Arum maculatum. A single charred tuber of this species may contain both solid cells (Fig. 8, Plate 54), cells with discernable cell contents (Fig. 6, Plate 55) as well as tissues that have undergone other types of preservation, (Plates 54 and 55). The tuber is large and irregular in shape. During charring the temperature attained within different regions of the tissue will be far more varied than in a narrow rhizome such as Anemone nemorosa.

5.6 CHARACTERS OF THE VASCULAR TISSUE

Vascular tissues often do not survive intact, consequently

cells solid as in tissue that has been charred from the fresh state, (Fig. 8, Plate 5).

The outer tissues of a dried rhizome char in a similar manner to the tissues throughout a rhizome charred from the fresh state. It is possible that the intense heat throughout a charring fresh (wet) rhizome and in the outer tissues of a dried rhizome cause the starch grains within the cells to fuse. A slower rise to a less intense heat at the centre of rhizomes dried prior to charring allows the cell contents to be preserved intact.

Similar charcoal results from the charring of tissues of the tuber Arum maculatum. A single charred tuber of this species may contain both solid cells (Fig. 8, Plate 54), cells with discernable cell contents (Fig. 6, Plate 55) as well as tissues that have undergone other types of preservation, (Plates 54 and 55). The tuber is large and irregular in shape. During charring the temperature attained within different regions of the tissue will be far more varied than in a narrow rhizome such as Anemone nemorosa.

5.6 CHARACTERS OF THE VASCULAR TISSUE

Vascular tissues often do not survive intact, consequently

detailed characters of the tissue are rarely of diagnostic value. Partial or complete breakdown of the vascular tissue is common, though the interpretation of the organization of these tissues is often necessary if an identification is to be reached. A number of different taxa illustrate the different characters of charred vascular tissue.

5.6.1 Complete Breakdown of the Vascular Tract

In the charred fleshy secondary roots of Potentilla anserina (Fig. 5, Plate 18) and in the root tubers of Ranunculus ficaria (Fig. 8, Plate 6) it is common for the whole of the central vascular tract to break down to leave a cavity with obviously fractured internal surfaces made up of cell wall debris. In other species where the vascular tissue is in bundles rather than a central vascular tract, the tissue can also partially break down, always beginning with the phloem. Often, however, the phloem is the only tissue to deteriorate leaving the elements of the xylem visible if rarely totally intact. This, as stated previously occurs in Scirpus maritimus (Fig. 8, Plate 48).

5.6.2 Deterioration of the Phloem

In cases where the phloem does not break down to leave a cavity, the tissue often becomes a solid indeterminable mass of carbon. Sometimes there are the faint recognisable remains of distorted cell walls, though more often the carbon has little texture. In most cases the region of deteriorated phloem is associated with a number of trachery elements which usually remain partially intact. In Alisma plantago-aquatica (Fig. 8, Plate 41), Dryopteris filix-mas (Fig. 4, Plate 2) and Alpinia galanga (Figs. 9 and 10, Plate 50) the phloem is reduced completely to solid carbon. In Anemone nemorosa the region of deteriorated phloem has faint distorted remains of cell walls, (Fig. 2, Plate 6). It is in a few isolated specimens of a few taxa that the tissue of the phloem is preserved intact, leaving it suitable for identification. Using characters other than its relative position to other vascular tissues.

5.6.3 Xylem

As a tissue xylem is usually preserved well enough to be recognised as such. Often the tracheal elements and if present, fibres, are preserved intact even if other tissues associated with the xylem are not. Xylem

parenchyma often deteriorates to a solid carbon on charring. In most cases though the details of the xylem is limited to its shape in transverse section and its width. The external walls are fused to the solid carbon of the surrounding deteriorated tissues. This phenomenon is well illustrated by the central tract of xylem in the root of Taraxacum officinale (Fig.6, Plate 39), xylem in vessel bundles in the root of Biebersteinia multifida (Fig. 4, Plate 21) and in the vascular bundles in the caudex of Alisma plantago-aquatica (Fig. 8, Plate 41). In some species the organization and preservation of the tissues allows the complete structure of the trachery elements to be seen. This is illustrated by the vascular bundles in the tuber of Tamus communis (Figs. 1 and 2, Plate 59) and rhizome of Nuphar advena (Figs. 9 and 10, Plate 4), meristeles in the rhizome of Pteridium aquilinum (Fig. 3, Plate 1) and rootstock of Dryopteris filix mas (Figs. 5 and 6, Plate 2) and in the tissue of the xylem in the root of Gentiana lutea (Fig. 8, Plate 28).

5.6.4 The Occurrence of Vascular Tissue

Since many of the organs referred to here are partly if not wholly storage organs, the major tissue within them is undifferentiated amyliiferous parenchyma. This contains

some vascular tissue, its position and concentration depending on the particular taxon. The chance of a fragment of a whole organ containing vascular tissue will therefore depend on the size of the fragment, its original position within the organ and the vascular characteristics of that taxon. Different species illustrate how this may vary.

In Armoracia rusticana where the vascular tissue of the stele is spread over at least two thirds of the width of the root and where the concentration of the vessels is very high, the chance of a fragment of a root containing xylem tissue is also very high, (Fig 8, Plate 13). In this case if a fragment of tissue contains no xylem it would also be too small for any other character to be of any use in identification. In this species the vascular tissue is important in identification by its concentration and position even if specific characters pertaining to the vessels are not apparent.

In Taraxacum officinale the xylem is collected into a central tract approximately a quarter of the width of the root. On charring this becomes very solid, the parenchyma between the vessel elements fusing to the vessel outer walls (Fig. 2, Plate 39). The tissues external to the xylem, composed of phloem and undifferentiated parenchyma

become very fragile on charring and are split by numerous tangentially oriented vesicles and tension fractures, (Fig. 1, Plate 39). These are easily destroyed leaving the charred central tract isolated and not easily recognisable as the remains of a fleshy root.

In many larger tuberous organs as well as some of the smaller tubers and rhizomes there is little vascular tissue. Its concentration is not high enough to ensure that many fragments will contain enough vascular tissue to allow an identification to be made based on vascular characters. This is particularly true when the vascular tissue is found, in many cases it is not preserved well enough for useful characters to be reliable. Arum maculatum and Tamus communis, both tubers, and Anemone nemorosa a narrow rhizome, all illustrate this problem well. If xylem is found then an identification may be possible but to rely on vascular characters for an identification is likely to leave the majority of charred fragments unidentified.

5.7 CHARACTERS OF THE PARENCHYMA

In charred tissue where the undifferentiated ground tissue of parenchyma is well preserved some characters may be

seen that are useful in identification. These may be defined as follows.

5.7.1 Cell Shape

The shape and size of individual cells varies within a tissue but an average size and shape is usually discernable since most of the parenchyma cells that make up a particular tissue are broadly similar. The cell shape may be described in terms of its roundness or angularity and the number of its faces. The outline of cells in transverse section, radial, longitudinal section and tangential longitudinal section may be of diagnostic value. The shapes, sizes and frequency of intercellular air spaces, if present, may also be typical of a species. Shrinkage and compression of tissues will cause artifactual or derived cell shapes such as the sinuous cell walls of Anemone nemorosa (Fig. 8, Plate 5) and Asphodelus aestivus (Fig. 7, Plate 57).

5.7.2 Cell Wall Characters

The shape of a cell after charring is character independent of whether the cell is empty, solid or contains determinable cell contents. The characters of the cell wall are not independent of these factors and

rely on the cell wall being visible and measurable. The middle lamella between cells does not survive charring, so the boundary between cells is not visible unless, as, for example, in the cases of Arum maculatum (Fig. 8, Plate 54), Doronicum grandiflorum (Figs. 5 and 6, Plate 35), Cyperus rotundus (Fig. 3, Plate 47) and Orchis mascula (Figs. 7 and 8, Plate 59), contraction of the cells allows the boundary to be seen. However in these cases the cells are solid after charring so the thickness of the cell wall is not determinable. In tissue where the cell wall is visible it may be charred so that it retains its natural thickness. It will appear very thin, fragile and probably fracture unevenly. This occurs in Scirpus maritimus (Fig. 5, Plate 48), Potentilla anserina (Fig. 6, Plate 18) and Asphodelus aestivus (Fig. 1, Plate 57). The cell wall may be unnaturally thickened to quite an extent, resulting in a much more solid charcoal, giving rise to a much more even fracture. This is more typical of the rhizomes of Butomus umbellatus (Fig. 1, Plate 41) and Pteridium aquilinum (Fig. 8, Plate 1), and the tuber of Arrhenatherum elatius ssp. bulbosum (Fig. 3, Plate 43). The increased thickness of the cell wall may be a result of the cell contents being compressed against the internal wall of the cell since the size of the cell is not increased, or may be due to cell wall expansion during the process of charring.

5.7.3 Cell Contents

The majority of cells in charred parenchymatous tissue are composed either of solid carbon or are devoid of any cell contents. The absence of cell contents does not necessarily mean that crystals, starch grains etc. are not normally present in the species.

Starch grains are commonly found in vegetative storage organs and are useful in identification in non-charred remains of similar tissues. Starch grains survive in few charred tissues and only in a few of these will the individual grains be discernable. Only following certain charring conditions will the starch grains be recognisable. With higher temperatures they will fuse and the cells will become solid. As previously stated this occurs in the rhizome of Anemone nemorosa and the tuber of Arum maculatum. When starch grains are preserved intact the size and shape are important characters in identification though the characteristic concentric rings around the hylam do not survive. Some examples of starch grain preservation are the small ovoid shaped grains in Ranunculus ficaria (Fig. 5, Plate 7), and rounded starch grains in the charred tissues of Withania somnifera (Fig. 8, Plate 29), Crambe maritima (Fig. 4, Plate 16) and Nuphar advena (Fig. 6, Plate 4).

There are several types of crystal in parenchymatous tissues, though in the charred tissues under observation here only raphides and druses were preserved. An example of raphide preservation is in the charred tuber of Tamus communis (Figs. 3 and 4, Plate 59). Examples of druse preservation are in the roots of Eryngium maritimum (Fig. 9, Plate 24), Polygonum bistorta (Fig. 2, Plate 11) and Rheum rhaponticum (Fig. 6, Plate 12).

5.7.4 Aerenchyma

In aerenchymatous tissues where chains or plates of often spherical cells form a tissue with large air spaces, the cells themselves often collapse on charring. This leaves a charcoal composed of what appear to be large irregular 'cells' the walls of which have the impression of cell walls upon them. The 'cell' is the cavity left by the collapse of the original cells around the large air spaces that made up the tissue, the new 'cell' lumen being the original intercellular air space. This type of preservation is illustrated by the charred tissue of the tuber of Alisma plantago-aquatica (Fig. 7, Plate 41), Schoenoplectus tabernaemontani (Figs. 9 and 10, Plate 47), Nuphar advena (Figs. 1 to 4, Plate 4) and Acorus calamus (Figs. 1 and 4, Plate 54). The shape of the 'cells' depends on the shape of the original intercellular air

spaces and differs between species. The total destruction of the aerenchymatous outer tissues of various species is dealt with below (section 5.11).

5.7.5 Idioblastic Cells

In some charred parenchymatous and aerenchymatous tissues idioblastic cells which, if differing from the surrounding ground tissue by their morphology rather than only by their contents and/or function, may be helpful in identification. The asterosclereides, such as are found in the aerenchyma of Nymphaea alba (Fig. 5, Plate 5), are preserved well on charring.

5.8 CHARACTERS OF THE MECHANICAL TISSUE

Organs composed largely of parenchyma do not usually contain much mechanical or sclerenchymatous tissue apart from that associated with the vascular system. Where mechanical tissue is present either as an independent tissue or associated with the vascular tissue it may be diagnostic in terms of its organization as well as the characters of the individual cells. Fibres of the sclerenchyma are well preserved on charring in the majority of cases, regardless of charring conditions. Mechanical tissue independent of the vascular tissue forms

a hollow cylinder separating the two concentric dictyosteles in the rhizome of Pteridium aquilinum (Figs. 4 and 5, Plate 1). Individual fibre bundles occur in the rhizomes of Typha latifolia and Typha angustifolia, (not illustrated - see section on Typha, Chapter six) and in the rhizomes of Sparganium species (archaeological material; Figs. 1 and 2, Plate 66). Fibres associated with the vascular tissue include the fibre caps of Alpinia galanga (Fig. 9, Plate 50) situated at the xylem pole; fibre bundles situated in the phloem and large amounts of fibre associated with the xylem in the vascular bundles of the rootstock of Polygonum bistorta (Fig. 7, Plate 10). In Oenothera biennis (Figs. 1 to 3, Plate 20), Lithospermum erythrorhizon (Fig. 10, Plate 29 and Figs. 1 and 2, Plate 30) and Cichorium intybus (Figs. 1, Plate 34), a large amount of sclerenchyma is associated with the secondary tissue of the xylem making the roots somewhat woody in nature.

5.9 SECRETORY STRUCTURES

Tissues that contain secretory structures such as laticifers or secretory ducts occur frequently in vegetative parenchymatous organs. In uncharred tissue they are useful aids to identification, but in charred tissue their preservation is too poor for use as

diagnostic characters. Laticifers occur in the tissues of many roots of Compositae, for example Scorzonera hispanica and Taraxacum officinale. The tissues containing laticifers range in the degree of preservation on charring, depending on the charring conditions, but even well preserved tissue contains no remains of these structures. Tissues containing secretory ducts such as are found in the tuber of Alisma plantago-aquatica may be well preserved but the remains of the ducts are not determinable amongst the other charred cellular remains. Secretory cavities, found for example in Inula helenium (Fig. 8, Plate 35) have been dealt with above.

5.10 CHARCOAL COLOUR, TEXTURE AND HARDNESS

Different parenchymatous tissues of different species and different tissues within the same organ may char to form charcoals of varying colours and textures. Colours range from black to grey although most fragments of archaeological charcoal are black. Charcoals may be brown, exemplified by the charred outer parenchyma of Raphanus sativus ssp. radiculata, although such charcoals are often very fragile possibly explaining their rarity amongst archaeological plant remains. A few species are significant in that they form charcoals of different colours. Biebersteinia multifida root charcoal is black

in colour but tinged with pink and the charcoal formed by the charring of the root of Withania somnifera is black with obvious white speckles.

Texture and hardness range from dull to glassy and from the very hard to very soft. Glassy charcoals tend to be very hard and often formed of vesicular charcoal or charred vascular tissue. Vascular tracts such as the meristeles in the rhizome of Pteridium aquilinum tend to be hard and glassy even though they are embedded in a charred ground tissue that forms a dull charcoal. Dull charcoals may be very hard, as in the charcoal of the root of Crambe cordifolia, or comparatively soft as in the charcoal of Alisma plantago-aquatica.

5.11 TISSUE DESTRUCTION

The total destruction of vesicular tissue in certain instances where cavities are left in a charred tissue has already been described. There may also be the complete destruction of parenchymatous tissues leading to the entire or partial destruction of the organ involved. Organs such as the fleshy petioles of Heracleum sphondylium, Rheum rhaponticum and Apium graveolens are reduced on charring to a fragile and friable charcoal whether the tissue is fresh or dried on charring. This

will easily deteriorate to ash on continued charring or to small fragments of unidentifiable charcoal if subjected to an external pressure. Other tissues unlikely to survive the process of charring are the fragile tissues of the aerenchymatous cortex of Typha latifolia, Alisma plantago-aquatica and Scirpus maritimus. Deterioration of these tissues, resulting in the complete or partial destruction is due to the large intercellular air spaces, little structural tissue and high water content. On charring vesicles develop within the tissue and since there is little strengthening tissue to prevent expansion, the charcoal splits into numerous very small fragments.

5.12 UNIDENTIFIABLE CHARCOAL

If a discernable cellular structure is present within a charred fragment of parenchymatous tissue, there is the potential for an identification based on anatomical characters or a combination of anatomical and derived artifactual characters. Clearly if there is no discernable cellular composition and no gross morphological characters on which to base an identification the potential to identify the charcoal even down to the family level is very low. It is rarely possible to base an identification on the derived artificial and artifactual characters of parenchymatous

tissue alone. Charred tissue that has no discernable composition is common amongst archaeologically preserved plant remains. This often appears as extremely vesicular carbon or solid glassy carbon and may be the result of charring tissues high in sugar content such as the parenchymatous content of some fruits. It is possible though for a very small fragment of either vesicular or solid charred tissues to result from almost any parenchymatous tissue, given the appropriate charring conditions for that taxon. For example the tissues of Arctium minus (Fig. 6, Plate 33) and Scorzonera hispanica (Fig. 1, Plate 37) which appear vesicular, would be unidentifiable by the methods presented here if presented as an isolated fragment.

5.13 NON-VEGETATIVE PARENCHYMATOUS ORGANS

Both anatomically and morphologically non-vegetative parenchymatous organs are more varied than those of vegetative origin. Endosperm, perisperm, cotyledonous parenchyma, parenchyma derived from the swollen receptacle or other parts of the inflorescence or any other parenchymatous tissue associated with the fruit or seed of a plant may be utilised medicinally or as food. In this section the results of charring four non-vegetative organs composed largely of parenchyma are described. These are

the fruit of Quercus robur, the acorn, a single seeded nut; the fruit of Ficus carica, the fig, a synconium; the fruit of Malus domestica, the apple, a pome; and the grains of Hordeum vulgare and Secale cereale, barley and rye respectively. In contrast to these the parenchymatous tissue of the gall of the Andricus spp. gall wasp formed on Quercus robur have also been charred and described here.

Whether fresh or dry the fruit of Quercus robur is preserved well on charring. The cellular structure remains intact although interrupted by the formation of cavities. The fruit is composed of two cotyledons forming two halves of the organ as seen in transverse section. The cavities radiate out irregularly from a line parallel to the long axis close to the centre of the flat internal surface of each cotyledon. This is illustrated by Figures 1 to 10 on Plate 60.

The dry gall or 'oak apple' formed on Quercus robur by the gall wasp, Andricus spp. is also preserved intact on charring. The outer parenchyma cells are rounded whereas the cells internal to this are radially elongated. These are illustrated by Figures 1 to 6 on Plate 61. Although the phloem deteriorates the vascular tissue also is preserved well. This can be seen in Figures 7 and 8 of

PLate 61. No vesicles or cavities are formed on charring although at the centre of the gall the cavity created by the gall wasp is preserved.

The results of charring the synconium type fruit of Ficus carica are similar whether the fruit is fresh or dried. All the tissues of the swollen receptacle become highly deteriorated due to the vesicularization of the parenchymatous tissues and the formation of solid masses of carbon and cavities. This is illustrated by Figures 9 to 10 on Plate 61 and Figure 3 on Plate 62. The elements of the xylem are preserved intact and are illustrated by Figure 4 on Plate 62. Attached to the internal walls of the swollen receptacle are the seeds which despite being partially covered in the vesicular remains of the receptacle tissue are preserved well. These are illustrated by Figures 1 and 2 on Plate 62.

The parenchymatous flesh of the 'pome' type fruit of the apple, Malus domestica, is also formed by the fusion of the hypanthium and the pericarp. Charred fresh this deteriorates totally to solid and vesicular carbon. To identify this tissue using anatomical criteria would be very difficult. When dried prior to charring however, the deteriorated remains of cell walls are visible although preservation is poor. Very large cavities form,

compressing the tissue into flat planes, the outer walls of which have the impression of cell walls upon them. No vascular tissue was observed in the charred state. Malus domestica is illustrated on Plate 62.

The caryopses of both Hordeum vulgare and Secale cereale illustrated on Plate 63 are archaeological remains. Readers are referred to the Materials section in Chapter 4. The state of preservation is however typical of modern cereal grains. While the shape of the grains is preserved intact the charred endosperm is not. This becomes highly vesicular and is not recognisable as parenchymatous tissue. Although the nature of the vesicular tissue differs between genera in terms of vesicle density and shape, in general terms the results of charring are similar.

The significance of charred non-vegetative parenchyma in the interpretation and identification of parenchymatous tissues in general, and vegetative parenchyma in particular, will be discussed in Chapter 8.

5.14 ANIMAL FAECES

The size and general rounded morphology of whole and fractured faeces of some animals may be similar to the

naked eye or under low power microscope to small or fragments of the larger charred vegetative parenchymatous plant organs under study in this thesis.

This section is not a guide to the identification of faecal material; it is here to illustrate that although fragments of dung and tuber may be superficially similar to the naked eye, they are easily distinguished under the microscope.

Taking as an example, goat dung, under the naked eye or low power magnification the outer surface seems smooth and inner surfaces of a broken fragment appear granular. Colour may vary from light brown to black. Under high magnification the outer surface appears rough and slightly granular although there are no recognisable tissues (Figs. 1 and 2, Plate 64). A fracture surface through the pellet reveals fragments of plant tissues, many with their long axis several times greater than their width. These are held together by much smaller fragments and a featureless carbon matrix. This is illustrated on Plate 64 by goat dung in Figures 3 to 7 and donkey dung in Figures 8 to 10.

The important feature that distinguishes animal, including human, faeces from fragments of intact plant tissue is the lack of organization of the constituent tissues (Hillman,

Madeystra and Hather 1988). Fragments of tissues and fibres run obliquely across each other, end abruptly and appear to have no structural relationship to each other. This cannot be said for even the most deteriorated fragments of vegetative parenchymatous tissue.

6.1 INTRODUCTION

In this chapter descriptions of each of the taxa under examination in this study will be given. This is with the exception of the non- 'root and tuber' tissues already described in the preceding chapter and the archaeological tissues described in the following chapter.

The sections devoted to each taxon will begin with a description of the gross morphology followed by details of the part of the plant under study. Following this will be a description of the charred tissues.

It must be noted that the descriptions of the fresh tissues are based on two separate considerations. Firstly the description must be full enough to ensure that an understanding of the organization of the tissues may be attained. Secondly, however, each description will contain no more information than is necessary to interpret the organization of the charred tissues and recognise diagnostic characters hopefully leading to an identification. Therefore the descriptions are not necessarily complete botanically though are adequate and precise for the purpose for which they are intended here.

Starch grains have been used in the identification of remains of parenchymatous tissues, (Ugent et al 1981, 1982, 1984, 1986, 1987) though these on the whole have been either dessicated or waterlogged, rather than charred. All the tissues under study here contain starch grains, though their preservation in the charred state is uncommon. When preservation does occur then details of the hylum and annular rings are lost and so their use in identification is minimised. For this reason, rather than describing the starch grains from all the taxa, only those in which preservation occurs will the starch grains be described. In these cases the charred state will be dealt with in the charcoal description for the relevant taxa.

Details relevant to the description of the fresh tissues may be found in the chapter devoted to the anatomy and morphology of vegetative parenchymatous organs (Chapter 3). Details relevant to the descriptions of the charred tissues may be found in the first chapter devoted to results (Chapter 5). Readers are also referred to the final section (4.4) in the Methods and Materials (Chapter 4).

6.2 PTERIDOPHYTES

PTERIDIUM AQUILINUM

HYPOLEPIDACEAE

Morphology The rhizome is cylindrical, 0.5 to 1.5 cm in diameter. Petioles emerge laterally from alternate sides of the rhizome giving an angular 'zig-zag' appearance. Fibrous roots emerge from the ventral surface.

Anatomy The rhizome is composed of an outer narrow epidermis internal to which lies a thickened hypodermis. Vascular and mechanical tissues lie in a ground tissue of undifferentiated parenchyma.

Epidermis: narrow, partially ruptured bearing hairs and scales.

Hypodermis: single to multiple layer of fibres internal to which lies a region of variously thickened parenchyma.

Ground Tissue: Divided into an outer and inner cortex and pith by concentric rings of an outer dictyostele, inner fibre ring and central dictyostele. Parenchyma cells are circular in transverse section 75 to 120 μm across. In longitudinal section these are barrel shaped 100 to 200 μm long elongated along the axis of the rhizome. Strands of fibres either singly or in groups of 2 to 3 are scattered throughout the tissue especially in the pith and the inner cortex.

Mechanical Tissue: A ring of fibres separates the two concentric dictyosteles; the latter are not entirely independant of each other implying the fibre cylinder is perforated (Foster and Gifford 1974). The cylinder narrows at two points laterally opposite each other. At its widest the fibre ring is up to 20 cells across, fibres with the largest lumen being towards the centre.

Vascular Tissue: The two concentric dictyosteles are each composed of between three and seven meristeles, the inner having fewer than the outer. Each meristele has an endodermis of a single layer of ill defined cells. There is no pericycle. The vascular tissue is organised in an amhicribal concentric arrangement. The phloem contains seive tubes up to 50 μm across. The xylem contains metaxylem elements up to 140 μm in transverse section the walls of which are up to 8 μm across. The xylem also contains a small amount of parenchyma. The meristeles may be circular in transverse section or elongated periclinally up to four times their width.

'Lateral Line': Watt (1979), has described regions of inner cortical parenchyma which intrude into the outer cortex along two lateral lines following the long axis of the rhizome. These are associated with the narrowing of the fibre ring described above. These together with a region of aerenchyma close to the apical meristem are,

according to Watt, concerned with rhizome aeration and remain functional only until maturation of the tissue.

Description of the Charcoal The rhizomes lose any hairs, scales and petiole remains on charring. The characteristic 'zig-zag' morphology is retained if not exaggerated by this loss. The charred rhizomes are no more than 1.2 cm across and most are less. Anatomically the rhizomes are altered little with the exception of certain points. The epidermis and hypodermis are turned to ash; the outer few cells of the cortex deteriorating to a friable and partially vesicular layer. The whole of the phloem endodermis and xylem parenchyma are reduced to solid carbon. This can be seen on Figures 1, 2, 5 and 6 on Plate 1. Tension fractures may form especially in tissues charred in a fresh rather than in a dried state, between the individual tissues of the sclerenchyma, meristemes and ground tissues. This may be seen on Figure 1 on Plate 1. Other than this there is little difference between tissues charred in the fresh and dried state. The ground tissue may be preserved well (Figs. 7 and 9, Plate 1) or become a little vesicular, (Fig. 8, Plate 1). Both xylem elements (Fig. 3, Plate 1) and fibres (Fig. 4, Plate 1) are preserved well. The charcoal is black in colour throughout, the xylem and sclerenchyma forming a glassy charcoal and the ground tissue a dull charcoal. Both are

hard and brittle.

DRYOPTERIS FELIX-MAS

ASPIDIACEAE

Morphology: the rootstock is cylindrical to conical in shape tapering away from the widest region a few centimetres behind the growing point. It is narrowest at the base where it gives rise to many fibrous roots. Surrounding the whole length of the rootstock are the persistent bases of dead rachises and light brown to orange scales. The rootstock is up to 15 to 20 cm across.

Anatomy: The rootstock is composed of an outer epidermis and hypodermis, vascular tissue and a parenchymatous ground tissue.

Epidermis: Narrow layer of partially ruptured cells bearing hairs and scales.

Hypodermis: A band of fibres up to ten cells deep. The walls are up to 8 μm across and the lumina up to 25 μm across.

Ground Tissue: Irregular, rounded parenchyma cells, few small intercellular air spaces. The cells are approximately 75 μm across in transverse section and elongated along the long axis up to 130 μm . Cell walls are thin. Ogura (1972) mentions the presence of glandular structures within the cells though these were not

observed.

Vascular Tissue: In transverse section the dictyostele is observed as a central ring of meristeles with lateral meristele rings leading to the rachises. The central ring may be made up of up to 20 meristeles, lateral rings fewer. Meristeles are between 200 μm and 1 mm across. An outer endodermis surrounds a pericycle 2 to 3 cells thick. The central vascular tract is organised in an amphi-cribal concentric arrangement. The xylem is made up of tracheids, 10 to 40 μm across, angular in transverse section as well as parenchyma.

Description of Charcoal: Both fresh and dried rootstocks produced similar charcoal. The epidermis, hypodermis and outer ground tissue deteriorate to a solid carbon layer between 100 and 700 μm across, (Figs. 1 to 3, Plate 2). Internal to this the charred ground tissue is vesicular (Fig. 3, Plate 2) only becoming recognisable as parenchyma internal to the main dictyostele, (Figs. 7 and 10, Plate 2). The meristeles are easily distinguishable, (Fig. 4, Plate 2). The endodermis, pericycle and phloem are reduced to solid carbon and are not discernable as individual tissue. The xylem parenchyma becomes solid but otherwise the xylem is preserved intact, (Figs. 5, 6, and 9, Plate 2). The charcoal is black in colour, the ground tissue being dull in appearance and the solid outer carbon

and the meristeles being glassy.

POLYPODIUM INTERJECTUM

POLYPODIACEAE

Morphology: The rhizome is cylindrical, 4 to 7 cm across growing either straight or curving in alternating directions. Petioles arise alternating from either side of the rhizome, their detachment leaving circular scars, 2 to 3 mm across. Fibrous roots occur ventrally where the rhizome touches the substrate.

Anatomy: The rhizome is composed of an epidermis, vascular tissue and a parenchymatous ground tissue.

Epidermis: Single layer of cells, the outer tangential wall is thickened and covered with a waxy cuticle.

Ground Tissue: Composed of parenchyma cells 80 μ m across in transverse section appearing as 4 to 8 sided polygons. Cells are elongated longitudinally up to 140 μ m, tapering slightly at either end. Walls are thin and intercellular air spaces are few.

Vascular Tissue: A single dictyostele is made up of 10 to 20 meristeles, roughly circular in transverse section, 100 to 450 μ m across. Parenchyma cells close to the endodermis are thickened along walls adjacent to the meristeles. Internal to an unthickened endodermis is a pericycle 2 to 3 cells thick. The vascular tissue,

internal to this is organised in an amphi-cribal concentric arrangement. The xylem is composed of tracheids varying between 8 and 35 μm across. These appear angular in transverse section.

Description of Charcoal: When charred dry the tissues are preserved almost intact (Figs. 1 to 4, Plate 3). Cells of the endodermis, pericycle and phloem are however reduced to solid charcoal (Figs. 5 to 7, Plate 3). Tissues charred from a fresh state may deteriorate considerably; the ground tissue being reduced to solid carbon (Fig 9, Plate 3) and by the formation of vesicles (Fig. 8, Plate 3). These are more or less circular in transverse section but are elongated along the long axis of the rhizome. The internal walls of the vesicles have the impression of compressed parenchyma cells upon them (Fig. 10, Plate 3). Both types of charcoal are soft, dull in texture and black in colour.

6.3 ANGIOSPERMS

6.3.1 Dicotyledons

NUPHAR ADVENA

NYMPHAEACEAE

Morphology: Both this and the following species Nymphaea

alba perenate by means of a swollen aquatic rhizome. This is homogenous along its length and circular in transverse section, between 2 and 3.5 cm across. The surface is covered in a complex close arrangement of peduncle scars. Their morphology and phyllotaxy have been examined by Cutter (1957).

Anatomy: Internal to a thick periderm is an aerenchymous ground tissue through which runs a truncated system of vascular bundles.

Periderm: 4 to 5 layers of highly thickened fibres.

Ground Tissue: Aerenchymous, made up of plates of irregular, rounded but more or less isodiametric cells packed with spherical starch grains. Cells are approximately 50 μm across. The intercellular air spaces formed by the network of plates are polygonal in transverse section 200 to 250 μm across and elongated along the axis of the rhizome up to 800 μm .

Vascular Tissue: Co-lateral vascular bundles run, apparently randomly throughout the ground tissue. The confusion of bundles is due to the truncated nature of the internodes along the length of the rhizome, (Arber 1920). The xylem is more or less circular in transverse section and made up of angular trachial elements 30 to 50 μm across. There is little xylem parenchyma. The phloem may occur internally, externally or laterally to the xylem as an ovoid extension to the vascular bundle as seen in

transverse section.

Description of Charcoal: Both dried and fresh tissues are similar after charring. The periderm has not been seen to survive the process of charring though the complex nature of peduncle scars is visible. The ground tissue is preserved intact (Figs. 1 to 5, Plate 4) and starch grains within the cells of the aerenchyma are also preserved, (Figs. 5 to 8, Plate 4). Vascular bundles are easily recognisable though the tissue of the phloem is reduced to solid carbon. The xylem is preserved intact (Figs. 9 to 10, Plate 4). The charcoal is black to brown in colour, dull in texture, soft and brittle.

NYMPHAEA ALBA

NYMPHAEACEAE

Morphology: The rhizome of this species is similar to that of Nuphar advena, previously described. It is circular in transverse section between 3 and 7 cm across. The morphology and complex phyllotaxy of the peduncle scars has been examined by Cutter, (1957).

Anatomy: Internal to a variously thickened peridermal region are periclinally oriented rectangularly shaped pockets of aerenchyma separated by walls of parenchyma. A central parenchymatous pith contains a polystelic vascular system. An endodermis is lacking (Metcalfe and Chalk

1950).

Periderm: This is made up of cubic to rectangular stone cells between 50 and 200 μm across. Parenchyma internal to this is tangentially elongated in transverse section and circular and longitudinal section.

Aerenchyma: Rectangular regions of aerenchyma situated in the outer tissues of the rhizome are made up of chains of long thin cells 50 to 100 μm long. These form regular intercellular air spaces up to 350 μm across. Situated within this tissue are characteristic asterosclereides 250 to 500 μm across. The sharply pointed arms are covered in small rectangular crystals. The arms may be straight or curved and grow in three dimensions.

Parenchyma: A parenchymatous ground tissue forms the pith and the 'walls' between the pockets of aerenchyma. The cells are more or less spherical 50 to 75 μm across. There are small regular intercellular air spaces.

Vascular Tissue: Between 10 and 20 steles lie in a ring internal to the aerenchyma. Each is formed of between 6 and 10 vascular bundles varying greatly in size and shape. Each bundle is made up of wedge shaped region of phloem and parenchyma tapering away from the centre of the stele as seen in transverse section. The tissue closest to the centre of the stele contains a number of trachial elements. These become fewer away from the centre of the stele. Trachial elements are 25 to 40 μm across and

circular in trasverse section.

Description of Charcoal: Tissue charred from the dried state is altered little anatomically by the process of charring. Periderm (Fig. 1, Plate 5), parenchyma (Fig. 2, Plate 5), aerenchyma (Fig. 4, Plate 5) and asterosclereides (Fig. 5, Plate 5) remain intact. The complex pattern of peduncle scars also remains undamaged by the process of charring. Vascular tissue is deteriorated greatly since it is composed of few trachial elements embedded in phloem and parenchyma. Tissue charred from the fresh state is preserved poorly. Many of the tissues deteriorate to a vesicular matrix (Fig. 3, Plate 5). The parenchyma survives to a greater extent and the characteristic asterosclereides are preserved intact. The charcoal in both cases is black througout slightly glossy in texture but relatively soft.

ANEMONE NEMOROSA

RANUNCULACEAE

Morphology: The rhizomes of this species are irregularly swollen being between 3 and 7 mm across and circular in transverse section. Narrow fibrous roots appear at the nodes on the ventral surface, the rhizome shoots from the dorsal surface. The epidermis is covered in a waxy cuticle. Bell and Sherrifs (1984) examined rhizome

branching patterns, growth and morphology in Anemone nemorosa.

Anatomy: Internal to a thick walled epidermis is a parenchymatous ground tissue in which is embedded a simple system of vascular bundles.

Epidermis: Single layer of square to rectangular cells 25 to 50 μm across. The outer tangential wall is thickened.

Ground Tissue: Parenchyma cells circular to polygonal in transverse section up to 80 μm across. Cells are elongated longitudinally up to 125 μm . There are few intercellular air spaces.

Vascular Tissue: A ring of vascular bundles, concentric with the epidermis, lies between one third and one half of the way across the radius of the rhizome. The ring commonly is made up of 5 to 8 bundles. The bundles are collateral, the phloem and the xylem tapering away from the widest point of the bundles at the vascular cambium. The xylem is composed of a few widely spaced thick walled polygonal vessels with circular lumina in transverse section. The vessels are approximately 20 to 25 μm across and associated with larger cells of xylem parenchyma.

Description of Charcoal: Tissues charred after being dried show significant differences from those charred from the fresh state. tissues that have been charred dry show better preservation than those charred fresh primarily in

the nature of the preservation of the starch grains in the parenchymatous cells of the ground tissue. The most intact form of preservation occurs at the centre of rhizomes dried prior to charring (Fig. 6, Plate 5) where starch grains and cell walls are all individually discernable (Fig. 10, Plate 5 and Fig. 1, Plate 6). Towards the outer tissues of such rhizomes the starch grains become 'gelatinised', individual grains are not discernable though the general rounded nature of the grains is visible in a few cells (Fig. 9, Plate 5). The outermost cells of the rhizome are solid carbon with no discernable cell contents (Fig. 7, Plate 5). The intercellular air spaces visible on Figure 8 (Plate 5) are typical of this form of preservation. In rhizomes charred from the fresh state the type of preservation is typified by solid cells and small intercellular air spaces occurring throughout the rhizome (Fig. 5, Plate 6). Large vesicles, rounded in transverse section and elongated longitudinally are also typical of rhizomes charred from the fresh state (Fig. 4, Plate 6). Vascular tissue preservation is similar in both fresh and dried charred tissues (Figs. 2 and 6, Plate 6). Phloem and xylem parenchyma deteriorate to solid carbon but the xylem elements are preserved intact. Morphologically the rhizomes change little. The charcoal is black throughout. Where preservation of the starch grains is good the

charcoal is dull and soft, where poor it is hard and glassy. In both cases it is rather brittle.

RANUNCULUS FICARIA

RANUNCULACEAE

Morphology: The primary root tubers of this species have been examined by Hacket (1927) who observes both aerial and root tubers as storage, perenating and propagating structures. Here, only the root tubers are under observation. The reader is referred to the work of Hacket for a more detailed and applied morphological examination of this species. The root tubers are attached to the plant just internal to the base of the stem. Up to 20 may be attached to a single plant but more commonly there are between 7 and 12. The tubers are narrow at their point of attachment at about 2 mm across. They gradually become wider until a point about five sixths along the length of the tuber where they may reach 6 or 7 mm across. They taper to a rounded end from this point. Tubers may be 5 mm to 8 cm in length, width changing little despite great variations in length. Tubers of all sizes appear on a single plant.

Anatomy: Internal to a narrow epidermis is a parenchymatous cortex and a central endodermis, pericycle and vascular stele.

Epidermis: Single layer of hyaline cells rectangular in

surface view and 25 μm deep. The surface has a thick cuticle. The epidermis is thicker, up to 60 μm at the distal end.

Cortex: Parenchyma cells, polygonal in transverse section varying in size from 35 μm across at the periphery to 125 μm close to the stele. In longitudinal section the cells are rectangular, elongated either radially or longitudinally, or are square 50 to 125 μm across.

Stele: Endodermis and pericycle are present, external to a pentarch vascular stele. The whole of the stele including the endodermis is approximately 320 μm across. The stele begins to differentiate at around 350 μm from the distal end of the tuber.

Description of Charcoal: As with the previous species Anemone nemorosa, there are significant differences between tissue charred from the fresh and from the dried state. Tissues charred after a period of drying are preserved either wholly intact (Fig. 7, Plate 6) but more often with the deterioration of the tissues of the stele (Fig. 8, Plate 6). In the latter case a cavity is left throughout the central tract of the tuber. The epidermis often deteriorates to a narrow layer of solid charcoal (Fig. 10, Plate 6) but the parenchyma of the cortex remains intact (Figs. 1 to 4, Plate 7). Starch grains are also preserved (Fig. 5, Plate 7). These are ovoid in

shape approximately 10 μm across. In contrast tissues charred from a fresh state deteriorate greatly. All of the internal tissues are compressed against the internal wall of the epidermis leaving the entire tuber as a single cavity (Figs. 8 and 9, Plate 7). The tissues of the cortex and stele are compressed into an extremely vesicular carbon (Fig. 10, Plate 7). The charcoal is black throughout dull to glassy in texture and relatively hard.

GYPHOPHILA STRUTHIUM

CARYOPHYLLACEAE

Morphology: The fleshy tap root of this species is narrowly tapering, up to 2.5 cm across at the widest point shortly internal to the root/stem junction. As with the majority of secondary roots under study in this research the function of the root of this species is perennation, storage and anchorage.

Anatomy: Between the periderm and the vascular cambium is a region of parenchyma and phloem. Internal to the cambium is a wide region of xylem. A parenchymatous pith forms the centre of the root. Parenchymatous rays radially traverse the root from the pith to the outer parenchyma. The cambium and the xylem/pith junction dissect the radius of the root into equal parts.

Periderm: Several layers of thickened cells.

Phloem/Parenchyma: Immediately internal to the periderm is a region of isodiametric parenchyma cells approximately 50 μm across, many containing druses. The phloem internal to this is radially dissected at regular intervals by parenchymatous rays. These widen towards the periserd causing the phloem to taper away from the cambium.

Xylem: Internal to a narrow cambium are radially oriented rows of groups of vessels dissected by parenchymatous rays. Vessels are 40 to 125 μm across, more or less circular in transverse section with circular lumina. The xylem parenchyma is circular in transverse section, 20 μm across but elongated longitudinally up to 100 μm . There may exist concentric rings of groups of fibres in the xylem, again dissected by the parenchymatous rays. The rays contain druses.

Pith: Largely parenchymatous made up of more or less isodiametric cells but also containing a few solitary vessels. Many cells contain druses.

Description of Charcoal: Dried and fresh tissue was observed to be similar on charring. The periderm was reduced to ash on all occasions. The phloem and parenchymatous region external to the cambium was highly deteriorated (Fig. 1, Plate 8) though the xylem due to its highly lignified nature was preserved well. The dissected form of the xylem by the parenchymatous rays is clearly

seen even though the tissue of the rays has deteriorated, (Fig. 2, Plate 8). The actual tissues of the xylem preserve well (Fig. 3, Plate 8) the xylem parenchyma becoming highly thickened and visible as almost solid carbon with small elongated vesicles. This is easily seen at the centre of Figure 3 (Plate 8). The pith deteriorates to a certain extent although druses in this tissue persist after charring. This charcoal is black to grey in colour, dull in texture but very hard.

BETA VULGARIS ssp. MARITIMA

CHENOPODIACEAE

Morphology: The root is a thick, fleshy, highly ramified secondary structure growing up to 30 cm long. Due to the ramification few of the limbs are more than 3 to 4 cm across, most being less. The surface may be smooth or transversely wrinkled.

Anatomy: Internal to a periderm is a parenchymatous ground tissue containing concentric rings of cambial and vascular tissue. The most central cambial ring has, internal to it, a solid core of xylem. Vascular tissues external to the innermost cambial and phloem cylinder are tertiary in origin. This form of anomalous growth is described in chapter 3 and has been described for the garden beet Beta vulgaris ssp. vulgaris by Artschwager (1926) amongst others.

Periderm: Variable in thickness composed of poorly thickened cubic cells 30 μm across. The outermost layer of cells tends to be somewhat broken.

Ground Tissue: Cells immediately internal to the periderm are circular to ovoid, tangentially elongated, 30 to 60 μm across in transverse section. These are elongated longitudinally 30 to 50 μm . Cells internal to the outermost cambial ring and throughout vary greatly in shape but measuring between 30 and 60 μm across. Some cells close to the central vascular tissues may reach 100 μm across.

Vascular Tissue: Concentric rings of cambial tissue give rise externally to phloem and internally to xylem. There may be up to eight concentric rings across a single root. The outermost rings are entire but contain little xylem tissue. Rings internal to this contain greater amounts of both phloem and xylem and so are wider though are divided into discrete vascular bundles. The innermost ring has a solid core of vessels and fibres. Vessels are circular in transverse section 20 to 65 μm across.

Description of Charcoal: The most striking feature of the charred tissues of this species is the persistence of the vascular rings and the deterioration of the parenchymatous ground tissue. Internal tissues that have been exposed directly to heat by fracturing of the root prior to

charring are illustrated by Figures 7 and 8 on Plate 8. Vascular rings are easily visible here. In tissues fractured after charring (Figs. 9 and 10, Plate 8 and 1 to 6, Plate 9), vascular tissues persist as rings of tissue whereas the ground tissue has deteriorated to form concentric rings of cavities. This is however disguised by the presence of radially oriented cavities emerging from the centre of the root. The central tract of xylem is visible on Figure 4, Plate 9. Longitudinal fracture surfaces indicate the compressed nature of the deteriorated ground tissue between the vascular rings (Figs. 5 to 6, Plate 9). The charcoal is black throughout, may appear either dull or glassy in texture and is hard.

BETA VULGARIS ssp. VULGARIS

CHENOPODIACEAE

Morphology: As one of the many forms of cultivated beets this taxon has been examined as a direct comparison between wild and cultivated related sub-species. The root is highly swollen non-ramifying and is widest several centimetres away from the shoot junction.

Anatomy: Artschwager (1926), Winton and Winton (1935) and Haywood (1938) have examined the anatomy of this taxon. It has basic similarities with B. vulgaris ssp. maritima though differs in respect to the relative amounts of

vascular and parenchymatous tissues.

Periderm: Similar to B. vulgaris ssp. maritima.

Ground Tissue: Similar though generally more uniform than B. vulgaris ssp. maritima being more or less isodiametric at 50 μ m across. Parenchymatous tissue between the vascular and cambial rings is wider.

Vascular Tissue: The number of vascular rings and their organisation is similar to that of B. vulgaris ssp. maritima.

Description of Charcoal: Unlike B. vulgaris ssp. maritima, deterioration of the parenchyma accounts for the formation of large vesicles in the charred tissues of this taxon. These large cavities form concentric rings between which may be seen narrow bands of compressed vascular tissue, primarily of the phloem (Figs. 7 to 10, Plate 9 and Fig. 1, Plate 10). The parenchyma deteriorates to varying degrees, apparently randomly throughout the root. This occurs irrespective of whether the root is dried, fresh, whole or fragmented prior to charring. Both good and poor preservation of the ground tissue is illustrated by Figures 2 to 5 on Plate 10. The charcoal is black to dull in texture and soft.

Morphology: The stout rootstock or erect rhizome is often sinuous in shape. It is unbranched and transversely is highly wrinkled. The specimens under observation were no more than 3 cm across.

Anatomy: Internal to a well developed periderm is an outer parenchymatous cortex. A ring of vascular bundles separates this from an inner parenchymatous pith.

Periderm: Radially oriented rows of 3 to 4 tangentially flattened cork cells the outermost of which are somewhat broken.

Cortex: Isodiametric parenchyma cells 20 to 40 μm across, many containing druses. In a rootstock 3 cm across the cortex was approximately 3 mm across.

Vascular bundles: These occur in a ring one quarter of the way across the radius of the rootstock. Internal to an outer cap of fibres 3 to 5 cells thick lies a region of phloem 100 to 200 μm across. Internal to narrow cambium lies a radially elongated region of xylem. This measured 100 to 200 μm across and 700 to 1100 μm deep. Internally this tapers gently to a rounded end. The xylem of each bundle contained 20 to 40 vessels ovoid to circular in transverse section and 25 to 40 μm across. These were embedded in a matrix of fibres. Vascular bundles are in

close proximity separated only by narrow parenchymatous rays many of the cells of which contained druses.

Pith: Accounting for two thirds of the width of the rootstock this is composed of ground tissue similar to that of the cortex and also containing druses.

Description of Charcoal: Both dried and fresh charred tissues were similar. The periderm is reduced to solid carbon (Fig. 8, Plate 10). The cortex though clearly parenchymatous becomes a little vesicular in places as does the tissue of the pith (Figs. 8 and 9, Plate 10). The druses throughout the tissue are preserved well (Fig. 2, Plate 11). The vascular bundles are easily discernable, the sclerenchyma and the xylem being preserved intact (Figs. 7 and 10, Plate 10, and Fig. 1, Plate 11). The tissues of the phloem and cambium are reduced to solid charcoal (Fig. 7, Plate 10). The charcoal is dull in texture and rather hard ranging in colour from black to grey to brown.

RHEUM PALAESTINUM

POLYGONACEAE

Morphology: The few specimens collected may represent young plants with rather smaller 'tap roots' than present on older and larger plants. The fleshy root is circular in transverse section, approximately 2.5 cm across,

transversely wrinkled and unbranched. Specimens were up to 20 cm long.

Anatomy: Internal to a substantial peridermal region lies a narrow region of phloem and parenchyma. The cambium forms an incomplete ring internal to which lies a region of xylem formed largely of parenchyma. The xylem forms approximately three quarters of the width of the root.

Periderm: A wide region of alternating layers of tangentially flattened unthickened cork cells and highly thickened stone cells. The stone cell layers may be highly distorted. A discernable phelloderm is visible as the innermost layer of the periderm.

Phloem/Parenchyma: The tissues of the phloem form narrow radially oriented rows of cells opposite similar rows of vessels in a largely parenchymatous xylem. The cambium forming an incomplete ring existing only between the strands of vascular tissue. The majority of the tissue above the cambium is parenchymatous made up of cells circular in transverse section 45 to 55 μm across. In longitudinal section these are circular to barrel shaped. Many of these cells contain druses.

Xylem: Radially oriented rows of vessels embedded in a wide parenchymatous matrix. The vessels are polygonal in transverse section with thick walls and circular lumina 15 to 85 μm across. The xylem parenchyma is similar to the tissue external to the cambium. The tissue of the xylem

also contains secretory ducts circular in transverse section with epithelial cells. The centre of the root is marked by a strand made up of several large vessels. The tissue contains many druses.

Description of Charcoal: Both fresh and charred tissues were similar. The preservation although not particularly good was characteristic for this and the following species R. rhaponticum. The tissues of the phloem and parenchyma above the cambium were reduced to a highly vesicular charcoal in which regions of solid carbon derived from phloem and the cambium persisted. The tissue of the xylem was again largely reduced to a mass of vesicular and partially solid charcoal though vessel elements persisted intact. Strands of vessel groups with their characteristic radial orientation are discernable (Figs. 3 to 5, Plate 11). In longitudinal fracture plane (Figs. 6 to 7, Plate 11) the characteristic pattern is less easily definable. The charcoal is soft and dull in texture ranging in colour from black to brown.

RHEUM RHAPONTICUM

POLYGONACEAE

Morphology: Though root tissue of the perenating organ of this species is a massively swollen secondary structure resulting from the tuberization of the 'tap root'. The

structure is basically cylindrical with many smaller roots emerging from the sides and the base. Shoots arise from the upper surface. The swollen root may reach 20 cm across and 30 to 40 cm long.

Anatomy: The smaller roots equal in size to the root of R. palaesinum previously described, are similar anatomically with the exception of a less heavily thickened periderm. Also no central tract of vessels has been observed in this species. The main body of the tuberous root is similar anatomically, the bulk of the tissue being that of the parenchymatous ground tissue of the xylem.

Description of Charcoal: Both dried and fresh charred tissues were similar. Preservation of the tissues as with the previous species was poor, though the characteristic pattern of radially oriented tissues was visible, (Figs. 9 and 10, Plate 11). Both tissues above and internal to the cambium deteriorated to a considerable extent. The tissues of the phloem and parenchyma internal to the periderm have deteriorated completely leaving a cavity, (Fig. 8, Plate 11). The vessel elements of the xylem tissue however may persist (Fig. 5, Plate 12), and druses persist even in the most damaged tissues (Fig. 6, Plate 12). Charcoal is similar to that of R. palaestinum.

Morphology: The root of Bryonia dioica is a massively swollen tuberous structure. The flat upper surface gives rise to a number of shoots each season. The lower surface gives rise to a number of short stout fleshy roots. The whole root may reach 15 cm across and 15 to 20 cm long.

Anatomy: Internal to a thick periderm lies a narrow region of parenchyma. Between this and the cambium is a narrow region of phloem. Internal to the cambium is a highly parenchymatous xylem taking up approximately six sevenths of the width of the root. Anomalous growth occurs within the tissue of the xylem.

Periderm: Several rows of tangentially flattened cork cells. These are unthickened and form a well defined layer approximately 150 μ m across.

Phloem/Parenchyma: Immediately internal to the periderm lies a region of parenchyma made up of tangentially elongated ovoid cells 50 to 100 μ m across. These are circular in longitudinal section 50 to 60 μ m across. The tissue of the phloem forms triangular regions tapering away from the cambium, intruding into the ground tissue internal to the periderm.

Xylem: Opposite each region of phloem lie narrow discrete bands of cambium internal to which lie radially oriented groups of vessels. The cambium is not continuous. Singly

or in groups of 3 to 4, vessels occur throughout the xylem which is largely made up of cubic to rectangular parenchyma cells 40 to 100 μm across. Associated with many of the vessel groups are narrow bands of cambial tissue giving rise to phloem and parenchyma. Vessels are polygonal in transverse section with polygonal lumina 30 to 50 μm across. Also present within the xylem are large breakdown cavities 3 to 4 mm across and lined with peridermal tissue.

Description of Charcoal: Both fresh and dried charred tissues were similar. The majority of the tissues of the root to a very large extent collapsed leaving large cavities enclosed by walls of highly compressed parenchymatous tissue. The outer tissues of the root were preserved in some cases (Figs. 7 and 8, Plate 12) though mostly these were compressed into narrow bands against the periderm leaving large cavities throughout the root, (Figs. 9 and 10, Plate 12 and Figs. 1 to 4, Plate 13). The walls of the cavities were seen to display the pattern of compressed parenchyma upon them (Fig. 5, Plate 13). The charcoal is black in colour, brittle, somewhat flaky and shiny.

Morphology: The secondary 'tap root' of this species is long and straight, usually unbranched and gives rise to several shoots above the transition zone. The root may grow up to 80 cm long and between 2 and 5 cm wide. It is transversely wrinkled.

Anatomy: Internal to a thin periderm is a narrow region of phloem and parenchyma. This region takes up only one sixth of the width of the root. Internal to a continuous cambium is a region of xylem occupying the rest of the root. Winton and Winton (1935) have examined the root of A. rusticana.

Periderm: This is made up of 2 to 3 layers of transversely flattened thickened cells. The periderm is rarely more than 50 to 60 μm thick.

Phloem/Parenchyma: Immediately internal to the periderm is a region of spherical to tangentially elongated cells 40 to 60 μm across. Stone cells in groups of 4 to 6 occur throughout this layer. Internal to this layer of parenchyma is a region of phloem and phloem parenchyma made up of radially oriented rows of cells. These rows extend occasionally into the outer parenchymatous tissue creating a rather 'zig-zag' boundary between the two tissues. The parenchyma cells within the phloem are longitudinally elongated up to 60 μm . Narrow bundles of

phloem sieve tubes occur throughout this tissue.

Xylem: This tissue lies internal to a continuous cambium and is composed of a parenchymatous matrix through which run many vessels singly or in groups of up to 6. A circular field of view 1 mm across may contain 40 vessels in 15 or so groups. Vessels are polygonal with polygonal lumina 25 to 50 μ m across. The ground tissue is similar to that of the phloem parenchyma.

Description of Charcoal: Both fresh and dried charred tissues were similar. The tissues external to the cambium become slightly distorted though the organization of the cells is clearly visible (Fig. 7, Plate 13). The phloem/xylem junction is apparent by the sudden appearance of vessels rather than the visible position of the cambium (Fig. 6, Plate 13). Both the cambium and the phloem deteriorate to solid carbon. The tissue of the xylem is very distinctive both in the concentration of vessels (Fig. 8, Plate 13) and the characteristic ground tissue (Fig. 9, Plate 13). The detail of the vessels is often preserved well (Fig. 10, Plate 13 and Figs. 1 to 2, Plate 14). The charcoal is black throughout, dull to glassy in texture and hard.

Morphology: The fleshy perennating organ of the turnip is made up of the swollen secondary root and hypocotyl of one of the many cultivated Brassica species. The variety examined here was globular in shape, almost spherical, approximately 10 across.

Anatomy: Between a narrow periderm and the cambium is a region of parenchyma and adjacent to the cambium, phloem. This layer is very narrow compared with the much swollen xylem tissues internal to the cambium. Anomalous growth of tertiary origin occurs within the tissues of the xylem. The anatomy of the turnip has been examined by Winton and Winton (1935).

Periderm: Narrow layer of cork cells.

Phloem/Parenchyma: Immediately internal to the periderm is a region of very varied parenchyma though generally tangentially elongated between 40 and 50 μm across. The phloem is restricted to a narrow region adjacent to the cambium. The cambium is continuous and in places up to 100 μm across.

Xylem: Groups of vessels are positioned opposite concentrations of phloem external to the cambium. The xylem is otherwise composed largely of parenchyma through which run isolated vessels and vessel groups. Associated with some vessel groups are cambia giving rise to tissues

of phloem and parenchyma. The xylem parenchyma is irregular in shape but generally isodiametric between 100 and 150 μm across.

Description of Charcoal: The charcoal resulting from the charring of whole or fragmented tissue of either fresh or dried tissue of this taxon is highly deteriorated and damaged. The possibility of reconstructing the organization of the tissues from the charred anatomy is very remote. Small regions of intact cellular remains persist (Fig. 4, Plate 14) but in general the tissues become solid and vesicular carbon and highly broken and deteriorated cellular remains with little or no organization. The charcoal is black to brown in colour soft and very friable. Unless the gross morphology can be determined identification of this taxon is difficult.

CRAMBE CORDEFOLIA

CRUCIFERAE

Morphology: This species perennates by means of a thick fleshy secondary root which tapers to a point from its widest region of 4 to 5 cm at the root/shoot junction over a length of up to 20 cm. Longitudinal ridges occur down the length of the root.

Anatomy: Between the periderm and a continuous cambium is a narrow region of parenchyma and phloem. Internal to the

cambium is a largely parenchymatous xylem.

Periderm: A narrow layer of cubic to rectangular cells generally unthickened and towards the outer surface somewhat broken.

Phloem/Parenchyma: Immediately internal to the periderm is a narrow layer of parenchyma internal to which are large rectangular regions of stone cells each 40 to 50 μm across. Parenchyma internal to this contains irregular bundles of fibres and adjacent to the cambium, regions of phloem. The parenchyma throughout this region is tangentially elongated to 50 μm across.

Xylem: Internal to the cambium and opposite each of the regions of phloem are radially elongated rays of vessels either singly or in groups, these are often associated with fibres. The number of vessels and fibres increases towards the centre of the root. At the centre of the root there is a solid tract of vessels and fibres. The xylem parenchyma cells are radially oriented, cubic in shape and up to 40 μm across.

Description of Charcoal: The charred tissue of the root of this species is a very dense almost solid carbon throughout. Vestiges of cellular patterns occur (Fig. 10, Plate 14 and Fig. 1, Plate 15) though the majority of the tissue is practically solid carbon with small vesicles, (Figs. 8 and 9, Plate 14). The vessels of the xylem

tissue are preserved intact (Figs. 2 and 3, Plate 15). The charcoal is black throughout, dull in texture and incredibly hard.

CRAMBE MARITIMA

CRUCIFERAE

Morphology: The secondary root of this species is very long smooth and narrow tapering gently from a width of 2.5 cm over a length of up to 80 cm. It is generally unbranched.

Anatomy: Internal to a thick periderm lies an outer region of parenchyma and a distinct inner region of phloem. Internal to the cambium is a region of xylem and depending of the region of the root varying amounts of parenchymatous pith.

Periderm: A thick layer of cork cells up to 200 μ m across external to which is a narrow layer of rectangular epidermal cells.

Phloem/Parenchyma: Immediately internal to the periderm is a region of irregular but generally transversely flattened cells up to 60 μ m across. Many groups of cells are ovoid in transverse section and divided periclinally up to three times along their length. Internal to this is a layer of radially oriented strands of phloem tapering away from the cambium and each capped with a groups of fibres.

Xylem: Internal to a continuous cambium are groups of

mostly large vessels embedded in a parenchymatous ground tissue. The vessels are arranged in radially oriented rays opposite each of the regions of phloem above the cambium. The vessels are rounded in transverse section and up to 100 μm across. The ground tissue is made up of cells rectangular in transverse section up to 50 μm across and elongated longitudinally up to 100 μm .

Pith: This varies in size becoming larger towards the transition zone. It is made up of cells isodiametric in transverse section 100 to 200 μm across and square to rectangular in longitudinal section irregularly storied.

Description of Charcoal: There is a considerable difference between tissues charred from a fresh state and tissues charred from a dried state. Tissues charred after drying are preserved well, the individual tissues easily discernable. The external region of parenchyma becomes semi-solid, the cell boundaries ill-defined although the lumina easily seen (Fig. 8, Plate 15). The phloem and the cambium become solid charcoal (Fig. 7, Plate 15). The tissue of the xylem is preserved well (Fig. 10, Plate 15 and Figs. 1 and 2, Plate 16). The parenchyma of the pith is preserved intact as are starch grains within the cells (Figs. 3 to 4, Plate 16). Preservation is less good in tissue charred from a fresh state. Radially oriented cavities occur in the xylem (Figs. 5 and 6, Plate 17) and

the cells of the pith deteriorate to a solid charcoal with irregular vesicles. Both types of charcoal are black throughout dull to glassy in texture and very hard.

RAPHANUS SATIVUS ssp. RADICULATA

CRUCIFERAE

Morphology: The fused secondary root and hypocotyl of this taxon has many cultivars. The cultivar under examination here is almost spherical between 1.5 and 3 cm across.

Anatomy: Internal to a narrow periderm is a wide parenchymatous layer with phloem adjacent to the cambium. Internal to the cambium the tissue of the xylem is largely parenchymatous with the addition of anomalous cambia and the resulting tissues of tertiary origin.

Periderm: Several layers of unthickened transversely flattened cork cells.

Phloem/Parenchyma: Internal to the periderm is a narrow region of irregular parenchyma made up of cells of many shapes and seemingly little common orientation. There are few intercellular air spaces and the cells range in size from between 30 to 120 μm across. Internal to this layer is a layer of phloem and phloem parenchyma. The tissue of the phloem itself forms triangular patches tapering away from the cambium. Between the regions of phloem are parenchymatous extensions of the outer ground tissue.

Xylem: The cambium is not continuous and is restricted to

the narrow rays of external phloem and internal rays of vessels. Parenchyma of the outer tissues extends into the tissue of the xylem. Vessels of the xylem are associated with the cambia giving rise to tissues both phloem and parenchyma. Winton and Winton (1935) examined this taxon.

Description of Charcoal: Preservation of tissues charred from the dried state and charred from the fresh state were significantly different. Tissues charred after drying were preserved in an extremely good condition with the exception of large cavities formed by tension fractures, often stretching across the whole root from one side to the other. Most fractures were however only a few millimetres wide. Intact preservation is illustrated by the outer tissues in Figures 8, 9 and 10 (Plate 16) and inner tissues in Figures 1 and 2 (Plate 17). Roots charred when fresh became one large vacuole all the tissues becoming compressed against the internal wall of the periderm. Charcoal produced by the charring of dried tissues is brown in colour, rather translucent and very soft.

CYCLAMEN PERSICUM

PRIMULACEAE

Morphology: The underground stem tuber of Cyclamen is derived from the swelling of the hypocotyl at the seedling

stage (Deffner 1978). Since the tissue is derived from a single internode it does not act as an organ of propagation but purely as storage, anchorage and perenation. The structure is circular in transverse section between 3 and 15 cm across but horizontally flattened up to a fifth of its width. Shoots appear from the upper flattened surface and fibrous roots from the lower.

Anatomy: The tuber has a thick periderm internal to which is a parenchymatous ground tissue throughout which is distributed a system of vascular bundles.

Periderm: Several layers of thickened cubic cells 40 to 50 μm across lie externally to between 2 and 4 layers of unthickened tangentially flattened cells in rows.

Ground Tissue: More or less isodiametric cells 60 to 100 μm across. There are a few intercellular air spaces. In a layer of ground tissue just internal to the periderm there are randomly distributed groups of 2 to 3 stone cells between 50 to 100 μm across.

Vascular Tissue: Vascular bundles are collateral up to 1.2 mm across the xylem being widely distributed away from the cambium. The region of xylem closest to the phloem is narrow and vessels are highly concentrated. Smaller vascular bundles also occur throughout the tissue. Bundles are apparently randomly distributed. Vessels are circular in transverse section approximately 25 μm across.

Description of Charcoal: Tissues charred from a charred state are preserved well so that individual tissues are discernable. However the outermost tissues of the periderm and outer ground tissue deteriorate to some extent, (Fig. 3, Plate 17). The parenchymatous ground tissue is preserved intact (Figs. 4 and 5, Plate 17) but the tissue of the phloem deteriorates to solid charcoal, (Fig. 6, Plate 17 and Fig. 1, Plate 18). The tissue of the xylem is preserved intact (Fig. 7, Plate 17). Tissue charred from a fresh state is rarely preserved intact the ground tissues undergoing distortion together with the formation of vesicles (Figs. 8 to 10, Plate 17). Compare Figure 5 (charred dry) and Figure 9 (charred fresh) on Plate 17. The charcoal is black throughout, ranges from dull to glassy in texture is soft and rather brittle.

POTENTILLA ANSERINA

ROSACEAE

Morphology: The secondary root of Potentilla anserina is a straight narrow structure rarely branching and giving rise to few lateral roots. It was never observed to be greater than 1 cm in width and narrowed to a fibrous root over a length of 12 to 18 cm. The surface is transversely wrinkled.

Anatomy: Internal to a thick periderm is a wide region of

alternating layers of parenchyma and phloem. There is a compact central tract of xylem and narrow pith.

Periderm: Internal to 2 to 3 layers of highly thickened layers of cubic cells are 4 to 6 layers of tangentially flattened unthickened cells.

Phloem/Parenchyma: This forms the majority of the tissue of the root being composed of alternate layers of wide bands of parenchyma and narrower bands of phloem. Between 6 and 9 concentric rings of phloem were observed in different specimens. The parenchymatous ground tissue is made up of tangentially elongated rectangular cells approximately 30 to 50 μm across in transverse section and 50 to 80 μm across in longitudinal section.

Xylem: Internal to the innermost ring of parenchyma is an almost complete ring of cambium internal to which lies tissue of the xylem made up of both vessels and parenchyma. Vessels are in groups of up to 4, circular in transverse section and 20 to 50 μm across. Internal to this is a narrow parenchymatous pith.

Description of Charcoal: Both dried and fresh charred tissues were similar. The charred anatomy of this species is striking in that all cases preservation of the soft tissues of the ground tissue and the phloem was good whereas the tissues that usually preserve well, the xylem, are deteriorated completely. The periderm is turned to

ash and is rarely preserved in any form. The alternate layers of parenchyma and phloem are intact (Figs. 3, 4, 6 and 8, Plate 18). The xylem and central pith deteriorate completely leaving a central fissure in the charred root (Fig. 5, Plate 18) or in the case of the emergence of lateral root xylem tracts, lateral fissures (Fig. 7, Plate 18). The charcoal is black throughout, soft and shiny.

Morphology: The root tubers of this species form as small, more or less spherical structures along the length of a fibrous root system. The tubers though, swellings along the root system, form an abrupt junction between the body of the tuber and the adjoining roots rather than a gradual one. The tubers were between 5 and 15 mm across.

Anatomy: The anatomy is basically similar to many fleshy secondary roots. Between the narrow periderm and the cambium is a narrow layer of parenchyma and adjacent to the cambium, phloem. Internal to the cambium is a large parenchymatous xylem with a central tract of vessels and fibres with rays of vessels between the cambium and the central tract.

Periderm: 1 to 4 layers of thickened cubic to spherical cells, irregular in width.

Phloem/Parenchyma: Immediately internal to the periderm is a region of parenchymatous cells tangentially flattened 20 to 40 μm across. These appear circular in longitudinal section 30 to 60 μm across. Intruding into this tapering away from the cambium are regions of phloem, triangular in transverse section. The phloem is widely spread around the cambium, each region being between 60 to 80 μm across but up to 2.5 mm apart.

Xylem: Internal to the cambium, opposite each of the

regions of phloem are radially oriented rays of vessels and fibres. The rays are up to 80 μm wide and emerge from a core of vessels and fibres at the centre of the tuber approximately 250 μm across. The xylem parenchyma is made up of radially oriented rows of square to rectangular cells in transverse section 30 to 50 μm across. These are polygonal in transverse section. Many of these cells contain rhomboidal crystals.

Description of Charcoal: Tissue charred from the fresh state and tissue charred from the dried state are strikingly different. Tissue dried prior to charring is preserved well though much of the tissue external to the cambium is somewhat distorted (Fig. 9, Plate 18). The xylem parenchyma is preserved intact (Fig. 10, Plate 18 and Figs. 1 and 2, Plate 19). There is also partial preservation of the starch grains within these cells (Figs. 3 to 4, Plate 19). In contrast tissues charred from the fresh state are deteriorated greatly. Much of the tissue is compressed against flattened rays of vessels radiating out from the central tract (Figs. 5 and 6, Plate 19). The outer tissues are reduced to solid carbon (Figs. 7 and 8, Plate 19), and the xylem parenchyma is compressed by large cavities the walls of which bear the impressions of parenchyma cells (Figs. 9 and 10, Plate 19). The charcoal is black to brown in colour and may be hard and

glassy or soft and dull in texture.

OENOTHERA BIENNIS

ONAGRACEAE

Morphology: This is a thick fleshy, occasionally branched secondary root. It is widest at the root shoot junction at approximately 2 cm tapering to a narrow point over a length of 15 to 20 cm. It is transversely wrinkled.

Anatomy: Internal to the periderm is an outer parenchymatous and inner phloem layer. Internal to the cambium lie vessels of varying sizes embedded in a parenchymatous matrix.

Periderm: 5 to 10 layers of unthickened cells in rows progressively becoming more flattened towards the external surface.

Phloem/Parenchyma: The outer region of parenchyma is made up of cells tangentially flattened in transverse section 20 to 50 μm across. These are elongated longitudinally and appear as storied parenchyma. Between this layer and the cambium is a continuous layer of phloem 50 to 80 μm across.

Xylem: The tissue of the xylem may be divided into four more or less equal regions. An outer layer of highly concentrated small vessels singly or in groups of up to 4, 25 to 45 μm across. Internal to this layer of much larger vessels up to 100 μm across. Internal to this a

layer of small vessels in low concentration 25 to 45 μ m across. The central tract of the root is made up of vessels up to 70 μ m across. All vessels have a high concentration of tyloses. The xylem parenchyma throughout the tissue is radially oriented rectangular and storied.

Description of Charcoal: Though a certain amount of distortion occurs on charring, especially in the tissue of the outer parenchyma caused by the deterioration of the phloem, most of the cell layers described above are preserved intact. Much of the xylem parenchyma takes on a rather sinuous form (Fig. 4, Plate 20) though the vessels themselves are preserved without distortion (Figs. 5 to 10, Plate 20). The charcoal is similar whether charred from the fresh or dried state. It is black to grey in colour soft and brittle, ranging from dull to shiny in texture.

BIEBERSTEINIA MULTIFIDA

GERANIACEAE

Morphology: The secondary root of this species is thick, fleshy and rather tuberous. It branches and tapers from its widest point a few centimetres internal to the root shoot junction. It tapers abruptly from a width of 4 to 5 cm over a length of no more than 10 cm

Anatomy: Between a thick periderm and a continuous cambium

is a narrow layer of phloem and parenchyma. Internal to the cambium is a wide region of xylem tissue composed largely of parenchyma containing radial rows of groups of vessels forming concentric rings and a central tract.

Periderm: This is made up of an external layer of highly thickened and partially distorted cells beneath which are several layers of tangentially flattened unthickened and somewhat distorted cells. Internal to this is a second layer of thickened cells. This is narrower and less distorted than the outermost cell layer.

Phloem/Parenchyma: Immediately internal to the periderm is a narrow layer of small thickened parenchyma cells. Internal to this is a wider region of cells, tangentially flattened in transverse section 50 μm across and circular in longitudinal section 30 μm across. The tissue of the phloem intrudes into this as triangular regions adjacent to the cambium and tapering away from it.

Xylem: Internal to a continuous cambium and opposite each of the regions of phloem are radially oriented groups of vessels forming concentric rings around a central tract of vessels. Each bundle contains between 5 and 20 vessels each 20 to 50 μm across. The central tract contains both vessels and fibres. The ground tissue of the xylem is composed of radially oriented ovoid cells in transverse section and irregular but rounded in longitudinal section 30 to 60 μm across.

Description of Charcoal: Tissues that have undergone a period of drying prior to charring are preserved in a manner that allows the distinctive organisation of the xylem tissue, though slightly distorted, to be seen. The outer tissues are to a large extent lost by the formation of vesicles at the level of the cambium (Fig. 2, Plate 21). The xylem parenchyma becomes solid and rather distorted (Figs. 5 and 6, Plate 21) but the distinct organization of vessels remains intact. Tissues charred from the fresh state collapse totally to form highly compressed tissues against the internal peridermal surface. This has the impression of xylem ground tissue cells upon it (Figs. 8 and 9, Plate 21). The charcoal is black to brown and tinged with pink ranging from dull to glassy in texture and is reasonable hard.

ERODIUM GLAUCOPHYLLUM

GERANIACEAE

Morphology: The perennating root tuber of this species lies at least 20 cm internal to the ground level attached to the aerial parts of the plant by a slender fibrous root. The tuber is 4 to 5 cm long, 1 to 1.5 cm wide and longitudinally flattened so causing it to be ovoid in transverse section. Fibrous roots emerge from the distal end in high concentration. The surface is generally smooth.

Anatomy: Internal to a thick periderm is a parenchymatous ground tissue continuous throughout the tuber. An incomplete ring of cambium lies about one quarter of the way across the radius of the tuber. External to this is the phloem and internally the xylem. Isolated vessels also occur throughout the xylem parenchyma as well as forming a narrow central tract.

Periderm: Internal to an outer layer of thickened and distorted cells is an inner layer of tangentially flattened and unthickened cells. Both layers are approximately 120 μm across.

Parenchymatous Ground Tissue: Made up of irregularly shaped angular cells up to 100 μm across in transverse section. These appear in longitudinal section as more rounded but still with few intercellular air space.

Vascular Tissue: The phloem occurs as narrow tapering regions external to short isolated vascular cambia. Directly internal to this are groups of vessels. Vessels are circular in transverse section and approximately 40 μm across. Isolated vessels occur throughout the xylem parenchyma as well as forming a central tract through the tuber.

Description of Charcoal: Tissues charred from the fresh state deteriorate beyond that which would normally survive the usual taphonomic processes. Tissues charred from the

dried state also deteriorate greatly. The resulting charcoal is extremely fragile and cellular remains are distorted. The periderm survives although cell walls are not visible (Fig. 10, Plate 21 and Fig. 1, Plate 22). The ground tissue is preserved with very thin friable walls and is distorted by the formation of vesicles (Figs. 1 and 2, Plate 22). Vascular tissue is preserved as solid carbon, derived from the phloem surrounding distorted xylem elements (Figs. 3 to 5, Plate 22). The charcoal is black in colour, dull in texture and extremely soft and fragile.

CONOPODIUM MAJUS

UMBELLIFERAE

Morphology: The perennating and storage organ of this species is a small generally spherical but irregularly shaped root tuber. The tuber is between one and three centimetres across and forms at the base of the stem up to 20 cm internal to the ground level. It gives rise to fibrous roots from small protrusion over its surface.

Anatomy: Internal to a periderm is a wide region of parenchyma with phloem adjacent to the cambium. Internal to the cambium the tissue of the xylem is largely parenchymatous with a diffuse organization of vessels and groups of vessels.

Periderm: Internal to an outer narrow layer of thickened

cells is a layer of tangentially flattened cells in rows. Together these layers may be between 8 and 12 cells across.

Phloem/Parenchyma: The ground tissue internal to the periderm is made up of polygonal and rectangular cells often in radially oriented rows. These are approximately 60 μm across. The outer region of this tissue contains numerous ducts with epithelial cells. Close to the cambium are rounded regions of phloem these are narrow and widely spaced.

Xylem: Internal to a wide and continuous cambium and opposite each of the regions of phloem are apparently random groups of vessels. These are circular in transverse section 15 to 20 μm across. Towards the centre of the xylem tissue the vessels become more diffuse and random in their organization. The xylem parenchyma is similar to that of the ground tissue external to the cambium.

Description of Charcoal: In a manner similar to that of Lathyrus linifolius tissues of this species when charred from the fresh state are compressed by the formation of vesicles radiating out from the centre of the tuber (Fig. 7, Plate 22). Tangentially placed vesicles also form within the outer parenchyma (Fig. 8, Plate 22). The central tissues of the xylem become a mass of solid carbon

and vesicles (Fig. 9, Plate 22). Preservation is better when tissues are charred from the dried state. The periderm and outer tissues survive but are highly distorted (Fig. 6, Plate 22). Central tissues generally become vesicular. The charcoal ranges from black to brown in colour, dull to glassy in texture and is rather soft.

DAUCUS CAROTA

UMBELLIFERAE

Morphology: The root of the carrot is composed largely of secondary root tissue although different varieties have varying amounts of tissue derived from hypocotyl. In most varieties it forms between one eighth and one twelfth of the structure. The variety chosen for examination was sharply tapering to a point from a width of 2 to 3 cm over a length of 15 to 20 cm. The surface was generally smooth.

Anatomy: Between a narrow periderm and a continuous cambium is a wide region of phloem and parenchyma derived from both the vascular cambium and the pericycle. Internal to the cambium is a central core of xylem made up largely of parenchyma. Numerous rays traverse the width of the root. The anatomy of the root of Daucus carota has been examined by Winton and Winton (1935), Havis (1939) and Esau (1940).

Periderm: This is narrow, made up of a single layer of

thickened cells 10 μm across.

Phloem/Parenchyma: Between the periderm and the cambium two distinct regions may be recognised. An outer region of tangentially elongated and transversely oriented cells up to 100 μm across: and an inner region of rectangular cells radially oriented and seen as storied parenchyma in longitudinal section. There is a certain amount of transition from one region to the other though a boundary is discernable. Oil ducts in the outer tissues observed by Esau (1940) were not found. Oil ducts and phloem were found in the inner region.

Xylem: Radially oriented rays of vessels lie internal to the cambium opposite similar rays of phloem external to the cambium. Throughout the xylem vessels lie randomly singly or in groups of 3 to 4. Vessels are circular 15 to 30 μm across. The xylem parenchyma is irregularly rounded and radially oriented in the outer xylem tissue but random towards the centre ranging from 50 to 100 μm across.

Description of Charcoal: Tissues charred from the dried state and tissue charred from the fresh state were found to be significantly different. Tissues dried prior to charring were well preserved with the exception of a certain amount of deterioration in the outer parenchyma and phloem caused by the formation of tangentially oriented vesicles (Fig. 10, Plate 22 and Fig. 1, Plate

23). The tissues of the xylem internal to the cambium may be preserved totally intact (Fig. 2, Plate 23) or with small radially oriented vesicles radiating out from the central axis of the root (Fig. 3, Plate 23). This contrasts with tissues charred from the fresh state where the formation of radially oriented vesicles in the tissues of the xylem often completely destroys any cellular remains within this tissue (Figs. 4 and 5, Plate 23). In tissues dried prior to charring the tissues of the phloem usually deteriorate and form large circular cavities around the region of the cambium (Fig. 6, Plate 23). In these cases the tissue of the xylem parenchyma is preserved intact (Fig. 7, Plate 23). Xylem parenchyma greatly deteriorates in tissues charred from the fresh state (Fig. 8, Plate 23). Vesicles in this tissue have the impression of parenchyma cell walls upon them (Fig. 2, Plate 24). The charcoal of both dried and fresh charred tissues is soft and brittle. Dried charred tissues tend to be brown in colour, especially the tissues of the outer parenchyma. Tissues charred from the fresh state are often black throughout and more brittle than tissues charred from the dried state.

ERYNGIUM MARITIMUM

UMBELLIFERAE

Morphology: This taxon has a long slender fleshy secondary

root that remains the same width over the majority of its length. Specimens measured 7 to 15 mm across. The root is longitudinally ridged.

Anatomy: Internal to the periderm is a wide region of parenchyma and phloem. The cambium is continuous with the exception of parenchymatous rays traversing the xylem, phloem and outer parenchyma. The xylem is narrow, there is a central pith.

Periderm: Internal to an external layer of broken, unthickened and tangentially flattened cells are several layers of thickened and tangentially flattened cells in rows.

Phloem/Parenchyma: Two distinct regions were observed. An outer region of tangentially elongated cells up to 70 μm across containing numerous oil ducts with epithelial cells; and an internal layer of isodiametric cells transected by rays. This tissue contains both oil ducts and phloem. Druses occur throughout both tissues and especially in the rays.

Xylem: A ring of vessels transected by rays lies internal to the cambium. Each region of xylem between the rays may contain up to 35 vessels each up to 50 to 75 μm across. The vessels are embedded in xylem parenchyma.

Pith: Parenchymatous cells circular in transverse section and rectangular in longitudinal section 50 to 90 μm across. Towards the outer region of this tissue is a ring

of oil ducts. Many of the cells of the pith contain druses.

Description of Charcoal: For both fresh and dried charred tissues the results of charring were similar. The periderm, though somewhat distorted is easily distinguished (Figs. 3, 4 and 6, Plate 24). The parenchyma and the phloem external to the cambium and the pith internal to the xylem both deteriorate greatly forming regions of solid carbon interdispersed with cavities. These are formed by both tissue breakdown and tension fractures, (Figs. 3 to 6, Plate 24). The tissue of the xylem is preserved intact forming a ring of vessel groups separated by distorted strands of solid carbon derived from the deterioration of the parenchymatous rays. Despite the deterioration of the parenchyma, druses are clearly visible within the solid carbon remains of the cells (Fig. 9, Plate 24). The charcoal is black throughout, soft and brittle.

HERACLEUM SPHONDYLIUM

UMBELLIFERAE

Morphology: The secondary root of this species is a thick fleshy occasionally branched structure. It tapers at a length of 30 cm from a width of up to 5 cm to a gradual point. It generally has a smooth surface.

Anatomy: Internal to a thick periderm is a wide region of parenchyma and phloem internal to which is a continuous cambium interrupted only by parenchymatous rays. Internal to the cambium is a wide region of xylem containing vessels, fibres and parenchyma. There is a narrow central pith.

Periderm: Wide and highly thickened layer of tangentially flattened cells in rows. The layer is approximately 300 μm across.

Phloem/Parenchyma: Rays dissecting this tissue persist close to the periderm. Between each of the rays adjacent to the cambium are regions of phloem. External to the phloem and internal to the periderm is a ground tissue made up of spherical cells becoming smaller towards the phloem. These range from 50 to under 10 μm across. Oil ducts occur throughout the tissue.

Xylem: Vessels, circular in transverse section 40 to 60 μm across occur singly or in groups of up to 9, are associated with both fibres and xylem parenchyma.

Description of Charcoal: Tissue charred from a fresh state and tissue charred from a dried state differ in a manner similar to that of Daucus carota. Tissues dried prior to charring are preserved well, individual tissues being easily discernable (Fig. 10, Plate 24 and Fig. 1 to 7, Plate 25). Tissue charred from the fresh state

deteriorates by the formation of vesicles radiating out from the central axis of the root (Figs. 8 to 10, Plate 25 and Figs. 1 to 2, Plate 26). This causes compression of the tissues into narrow rays of almost solid carbon (Fig. 9, Plate 25). The internal wall of the vesicles are highly distorted but impressions of storied parenchyma are visible upon them (Fig. 6, Plate 26). The charcoal is black throughout dull to glassy in testure brittle and rather hard.

MYRRHIS ODORATA

UMBELLIFERAE

Morphology: The secondary root of this species is highly swollen and branched. It tapers from a wide region several centimetres away from the root/shoot junction. Each branch of the root may be up to 4 cm across and up to 15 to 20 cm long. The root may be up to 10 cm across prior to branching and up to 25 to 30 cm long overall. It is highly transversely wrinkled.

Anatomy: Between a thickened periderm and continuous cambium is a wide region of parenchyma and internal to this a wide continuous region of phloem. Internal to the cambium is a region of xylem and internal to this a wide pith.

Periderm: Between 2 and 5 layers of thickened cells in

discrete rows. The periderm is highly distorted in regions.

Phloem/Parenchyma: The outer region of parenchyma and inner region of phloem and phloem parenchyma are more or less equal in width. Oil ducts with epithelial cells occur throughout both tissues. The parenchyma throughout both tissues is more or less rectangular in transverse section and appears as storied parenchyma in longitudinal section.

Xylem: Restricted to a narrow region internal to the cambium and made up of vessels circular to polygonal in transverse section 30 μm across embedded in a parenchymatous matrix.

Pith: Composed of radially elongated cells towards the xylem and circular cells at the centre as seen in transverse section. In longitudinal section the cells appear as storied though somewhat disorganised parenchyma. Cells measure 30 to 60 μm across.

Description of Charcoal: In a similar way to both Daucus carota and Heracleum sphondylium dried and fresh charred tissues of this species differ considerably. Tissues dried prior to charring preserve well, individual tissues being discernable as described above. Tissues charred from a fresh state undergo alteration caused by vesicle formation. Vesicles are tangentially oriented external to

the cambium (Fig. 9, Plate 26) and radially oriented internal to the cambium (Fig. 10, Plate 26 and Figs. 1 and 2, Plate 27). Little tissue compression occurs but rather the breakdown of tissues caused by tension fractures (Fig. 2, Plate 27). Tissues away from such fractures are preserved more or less intact (Figs. 3 and 4, Plate 27). Charcoal is black to grey in colour and reasonably soft.

PASTINACA SATIVA

UMBELLIFERAE

Morphology: The wild rather than the cultivated variety was examined here. The root of this is a slender tapering occasionally branched secondary structure. It tapers to a fibrous root from a width of 2 cm over a length of up to 30 cm. It has a smooth surface.

Anatomy: Between a thick periderm and continuous cambium is a wide region of parenchyma and phloem both with oil ducts. The tissue is transected by parenchymatous rays. Internal to the cambium is a central core of xylem. Waring (1934) examined this species.

Periderm: 15 to 20 layers of tangentially flattened cork cells only the outer few of which are thickened.

Phloem/Parenchyma: Internal to an outer region of tangentially elongated cells up to 50 μ m across is an inner region of radially elongated cells 30 to 40 μ m across. This inner region contains the tissue of the

phloem and is transected by parenchymatous rays. Oil ducts occur throughout these tissues.

Xylem: Internal to a wide and continuous cambium lies a central core of xylem, largely parenchymatous but containing radially oriented rays of vessels toward the outer tissue and a diffuse to apparently random organization of vessels toward the centre of the root. Vessels are circular to ovoid 30 to 50 μm across. The xylem parenchyma is storied in longitudinal section, rectangular to ovoid in transverse section 30 to 60 μm across.

Description of Charcoal: Despite the close anatomical similarities with other Umbelliferous roots under examination here, the dried and fresh charred tissues of Pastinaca sativa are preserved in a different manner than would be otherwise expected. The periderm is either lost (Fig. 5, Plate 27) or becomes thickened and persistent (Fig. 7, Plate 27). The parenchymatous ground tissue internal to the periderm is, with the exception of tangentially oriented tension fractures, preserved intact (Fig. 7, Plate 27 and Figs. 1 to 2, Plate 28). The phloem and cambium are deteriorated to a thick solid band of carbon (Fig. 8, Plate 27). The xylem is also to a large extent solidified with the exception of the lumina of the vessels and small regions of the xylem parenchyma close to

the centre of the root, (Figs. 9 and 10, Plate 27 and Figs. 3 and 4, Plate 28). The charcoal is black throughout ranging from dull to glassy in texture and is hard and brittle.

GENTIANA LUTEA

GENTIANACEAE

Morphology: The secondary root of this species is fleshy and moderately swollen with transverse ridges along its length. It gently tapers from a width of approximately 3 cm at the root/shoot junction.

Anatomy: Between the thick periderm and the cambium is a narrow region of parenchyma and phloem. Internal to the cambium is a wide region of xylem and a central parenchymatous pith. Wide rays transect the whole radius of the root.

Periderm: Internal to an outer region of five to six layers of distorted thickened cells, more or less cubic in shape are 4 to 5 layers of unthickened cubic cells in rows.

Phloem/Parenchyma: The outer parenchymatous region internal to the periderm is made up of cells circular in transverse section 30 μm across and elongated in longitudinal section up to 100 μm . Internal to this and adjacent to the cambium are regions of phloem tapering

towards the periderm. These are transected by the parenchymatous rays.

Xylem: Internal to the cambium is a wide region of xylem made up of both vessels and parenchyma. Groups of vessels opposite each of the regions phloem taper towards the centre of the root. Vessels decrease in size away from the cambium, the largest being 50 μm across. These are polygonal in transverse section with circular lumina.

Pith: This is a wide region of parenchyma made up of isodiametric cells 60 to 70 μm across.

Description of Charcoal: Preservation of both dried and fresh charred tissue is similar. The periderm is reduced to a solid layer (Figs. 5 and 6, Plate 28) and the parenchyma and phloem external to the cambium become a somewhat distorted and compressed layer (Figs. 5 and 6, Plate 28). The phloem/xylem junction is marked by a solid carbon ring derived from the deteriorated cambium and part of the phloem tissues. the xylem parenchyma does not survive well though the vessels are easily distinguishable amongst the remains of the parenchyma (Figs. 7 to 9, Plate 10). The preservation of the pith is similar to that of the xylem parenchyma (Fig. 10, Plate 28). The charcoal is brown to black in colour dull in texture hard and rather brittle.

Morphology: The storage and perenation organs of this species is a tuberous, fleshy swollen regions of the root system. The tubers are 1 to 2 cm wide and between 5 and 15 cm long and are not necessarily terminal on the root system. Atal and Schwartang (1961) state that there is variation between wild and cultivated roots of this species. Wild roots were observed to be less uniform than cultivated roots. It is not known whether the roots under examination here were wild or cultivated though since they varied little except in overall size it may be assumed that they were cultivated.

Anatomy: Internal to a narrow periderm is a layer of parenchyma containing small amounts of phloem adjacent to a thin and continuous cambium. Internal to a cambium is a central mass of parenchyma containing radially oriented rows of xylem close to the cambium and opposite each of the regions of phloem. Isolated vessels and a central core of vessels also occur within the xylem parenchyma.

Periderm: Up to 3 cell thick layer of slightly thickened cubic cells.

Phloem/Parenchyma: The ground tissue is more or less isodiametric 30 to 60 μ m across occupying approximately one fifth of the width of the root. Intruding into this tissue from the cambium are triangular regions of phloem

tapering towards the periderm.

Xylem: The cambium is continuous. Internal to the cambium and opposite each of the regions of phloem are radially oriented rows of vessels. These are either isolated or in groups of up to 4. The vessels are circular to polygonal in transverse section 40 to 50 μm across. The xylem parenchyma is made up of radially arranged rows of cells circular in transverse section 40 to 50 μm across. In longitudinal section these appear storied, elongated longitudinally up to 100 μm . The cells are less organised at the centre of the root.

Description of Charcoal: The preservation of dried and fresh charred tissues is similar. The periderm is indeterminable in the charred tissues. The outer and inner ground tissues of the phloem and the xylem are both preserved intact as are their contents of starch grains, (Figs. 1 to 8, Plate 29). The starch grains are ovoid to spherical but are preserved without any external morphology. The vessels of the xylem are preserved intact, (Figs. 3 and 9, Plate 29). The tissue of the phloem deteriorates to small indeterminable patches of solid carbon. The charcoal is grey with white speckles, dull in texture and hard.

Morphology: The secondary root of this species is a straight narrow fleshy structure with many lateral roots. It has longitudinal grooves down its length and tapers from its widest point of 1 to 2 cm at the transition zone.

Anatomy: Between a thick periderm and a continuous cambium is a narrow region of parenchyma and phloem. Internal to the cambium is a woody xylem and central parenchymatous pith.

Periderm: Several layers of tangentially flattened cork cells, partially distorted in regions.

Phloem/Parenchyma: This is a narrow layer of parenchyma containing adjacent to the cambium a near continuous region of phloem. The cells of the ground tissue are rectangular in transverse section and storied in longitudinal section up to 50 μm across.

Xylem: Internal to a continuous cambium is a woody xylem made up of short fibres up to 200 μm long and vessels polygonal in transverse section 50 μm across.

Pith: This is made up of irregular shaped parenchymatous cells up to 25 μm across. The pith contains individual vessels apparently randomly placed throughout the tissue.

Description of Charcoal: Both dried and fresh charred tissues were similar. The tissues external to the cambium

deteriorate to a narrow region of distorted charcoal (Fig. 10, Plate 29). The tissue of the xylem is preserved intact, (Figs. 1 to 3, Plate 30). The pith deteriorates to a cavity marked by a compressed wall of tissue adjacent to the xylem (Fig. 4, Plate 30). The charcoal is hard dull in texture and ranges from black to brown in colour.

SYMPHYTUM OFFICINALE

BORAGINACEAE

Morphology: The root of this species is a thick fleshy secondary structure branching little and tapering from a width of 2 to 4 cm to a fibrous tip over a length of up to 30 cm. The surface is smooth.

Anatomy: Internal to an outer periderm is a region of parenchyma containing, close to the cambium, regions of phloem. Internal to a continuous cambium is a largely parenchymatous xylem. The width of the xylem and phloem are more or less equal.

Periderm: 5 to 10 layers of tangentially flattened cells alternately placed rather than in rows.

Phloem/Parenchyma: The parenchymatous ground tissue progresses from rectangular, radially elongated and oriented in radial rows close to the cambium to tangentially elongated and tangentially oriented cells adjacent to the periderm. In longitudinal section these are rectangular and storied between 50 and 200 μm across.

Phloem occurs in a continuous layer adjacent to the cambium.

Xylem: The cambium is continuous and rather sinuous. Internal to the cambium are radially oriented rows of vessels giving way to randomly placed vessels at the centre of the root. Vessels are polygonal in transverse section 20 to 75 μm across. The xylem parenchyma is oriented in radial rows and appears as storied parenchyma in longitudinal section 30 to 60 μm across.

Description of Charcoal: Tissues charred from the fresh state and from the dried state differ significantly. This may be seen by comparing the charred outer parenchyma of dried tissue (Fig. 5, Plate 30) with charred fresh tissue (Fig. 7, Plate 30) and charred central xylem parenchyma of dried tissue (Fig. 6, Plate 30) with fresh tissue (Fig. 6, Plate 30). Charred dried tissue is generally preserved intact whereas charred fresh tissue is deteriorated by the formation of tangentially oriented vesicles in the outer tissues and radially oriented vesicles in the xylem parenchyma. The charcoal is black in colour glassy and shiny in texture and generally hard and brittle.

CISTANCHE TUBULOSA

OROBANCHEACEAE

Morphology: Typical of many members of this family is the

growth habit exhibited by this species. The inflorescence spike is an erect fleshy unbranched axis 20 to 45 cm high and 5 to 8 cm across. This extends internal to the ground up to a further 30 cm ending in a swollen base up to 15 cm across. A short region external to the swollen base is somewhat narrowed. The aerial axis is covered with peduncle scars.

Anatomy: Internal to a single celled epidermis is a parenchymatous cortex and pith divided by a sinuous ring of vascular bundles. The pith has a number of vascular bundles running randomly through it.

Epidermis: Single layers of radially elongated cells 40 μm deep and 17 μm wide in transverse section. In longitudinal section the cells are up to 100 μm long. There is a thick cuticle.

Ground Tissue: The ground tissue of the cortex and the pith is similar. It is made up of cells circular in transverse section 20 to 60 μm across. These are longitudinally elongated up to 450 μm . There are large intercellular air spaces.

Vascular Tissue: A sinuous ring of vascular bundles occurs about one fifth of the way across the radius of the root as well as larger vascular bundles within the pith. Bundles in the vascular ring are collateral with regions of both external phloem and internal xylem tapering away from an indistinct cambium. Vessels are thin walled,

polygonal in transverse section with circular lumina. Bundles in the pith are concentric with an amphivasal organization of the tissues. The xylem ring was never observed to be complete and the phloem is composed of large quantities of parenchyma. Bundles of the vascular ring measure on average 250 μm across whereas bundles of the pith measure on average 350 μm across.

Description of Charcoal: Tissues charred after a period of drying were preserved in a better condition than those charred from a fresh state. Tissues of inflorescences dried prior to charring showed most cell layers to be intact (Figs. 1 to 4, Plate 31), with the exception of the tissue of the phloem (Fig. 5, Plate 31) which is seen as a solid layer of carbon within the vascular bundle. Tissues charred from the fresh state are distorted by the formation of large vesicles (Fig. 6, Plate 31). The ground tissue becomes compressed and partially solidified (Fig. 7, Plate 31). The charcoal is brown in colour dull in texture and rather soft and fragile.

ANACYCLUS PYRETHRUM

COMPOSITAE

Morphology: The secondary root of this species is a fleshy secondary structure tapering over a length of 15 to 20 cm from a width of 2 to 3 cm at the root junction. It is

transversely ridged and gives rise to narrow lateral roots.

Anatomy: Internal to a narrow periderm is a region of parenchyma and phloem. Internal to a discontinuous cambium is a wider region of xylem and a central pith.

Periderm: 3 to 6 layers of tangentially flattened cork cells. Within this tissue are groups of up to 20 stone cells, cubic in shape 40 to 50 μm across.

Parenchyma/Phloem: Parenchyma immediately internal to the periderm is tangentially elongated becoming more spherical towards the cambium. Intruding into this tissue are triangular regions of phloem adjacent to the cambium and tapering towards the periderm. Within the parenchymatous tissue and lying alternately with the phloem and large more or less spherical secretory cavities lined with epithelial cells. The cavities are up to 125 μm across and several may be aligned in radially oriented rows.

Xylem: Opposite each of the regions of phloem and internal to the cambium are radially oriented rows of xylem vessels. The cambium is not continuous and it lies between the vascular tissue only. Between each of the rays of xylem is a ground tissue containing radially oriented rows of secretory cavities. The xylem contains thick walled vessels, polygonal in transverse section with circular lumina 10 to 40 μm across. Vessel rays are

widest at the cambium where they are up to 7 vessels across. Vessels are surrounded by xylem parenchyma.

Pith: Circular to rectangular cells in transverse section 40 to 45 μm across. These are more or less storied in longitudinal section.

Description of Charcoal: Both fresh and dried charred tissues were seen to be similar. A certain amount of distortion of the tissues occurs on charring although the individual tissues described above are discernable. The periderm rarely survives but tissues immediately internal to it are preserved and may be identified by the high concentration of secretory cavities (Figs. 1 to 3, Plate 32). The epithelial cells of the cavities are reduced to solid carbon. A solid layer of carbon is visible at the base of the outer tissues derived from the cambium and the phloem. The tissue of the xylem is preserved well, with the exception of the formation of vesicular cavities radiating out from the central long axis of the root in the parenchymatous tissues between the rays of xylem (Fig 10, Plate 31). The shape of the vessels is easily seen within the tissue of the xylem (Figs. 4 and 8, Plate 32). Tissue of the pith is also preserved well (Figs. 5 to 7, Plate 32). The charcoal is black in colour, dull in texture, hard and brittle.

Morphology: The root of this species is more or less unbranched fleshy secondary structure, tapering over a length of up to 60 cm from a width at the root/shoot junction of 5 to 6 cm. The surface is smooth. Winton and Winton have examined this species (1935).

Anatomy: Between a thick periderm and a continuous cambium are an outer layer of parenchyma and an inner layer of phloem. Internal to the cambium is an outer region of xylem and an inner pith containing randomly placed vessels.

Periderm: 3 to 4 layers of variously thickened distorted and tangentially flattened cells.

Phloem/Parenchyma: The outer layer of parenchyma is tangentially elongated but becomes circular in transverse section towards the inner layer of phloem. The cells are storied in longitudinal section 30 to 60 μm across. The phloem is continuous where it is adjacent to the cambium but tapers into peaks intruding into the outer layer of parenchyma. Within the phloem, just internal to each peak is a bundle of fibres 200 μm across.

Xylem: Internal to the cambium and opposite each of the fibre bundles in the phloem are radially oriented rays of xylem one vessel wide. Vessels are circular in transverse section 40 to 45 μm across. The xylem parenchyma contains

small groups of fibres and is radially oriented in transverse section, storied in longitudinal section.

Pith: This is similar to the xylem parenchyma although cells are larger, up to 100 μm across. Individual vessels are randomly placed within the tissue.

Description of Charcoal: Preservation of tissue dried prior to charring is generally good, individual cells of all tissues with the exception of the phloem and the cambium are easily distinguishable (Figs. 9 to 10, Plate 32 and Figs. 1 to 5, Plate 33). Tissues charred from the fresh state become semi-solid and rather vesicular (Fig. 6, Plate 33) and although such charcoal may be associated with better preserved regions of the same root individual fragments of tissue preserved as poorly as is shown here are not identifiable. As with much charcoal derived from roots of the Compositae this charcoal is black in colour dull in texture, hard and brittle.

CICHORIUM INTYBUS

COMPOSITAE

Morphology: The secondary root of this species is a narrow tapering structure up to 30 cm long and 1.5 cm across at its widest. It branches little and has a smooth surface. Knobloch (1934) examined this species.

Anatomy: Internal to a narrow periderm is a region of parenchyma and phloem. The cambium is continuous with the exception of narrow parenchymatous rays transecting the root. Internal to the cambium is a region of almost woody xylem. There is a central pith containing randomly placed vessels.

Periderm: Narrow layer of transversely flattened cells. These are partially thickened and somewhat distorted.

Phloem/Parenchyma: The outer parenchyma is rectangular to spherical, slightly tangentially elongated in transverse section and irregularly storied in longitudinal section. The phloem forms a narrow continuous layer transected by parenchymatous rays.

Xylem: The cambium is continuous with the exception of the rays. The xylem is made up of wide regions of vessels surrounded by a ground tissue of fibres. This is transected by parenchymatous rays. Vessels are circular to polygonal in transverse section and 25 to 50 μm across.

Pith: This is made up of irregularly shaped parenchyma containing vessels singly and in groups, apparently randomly placed throughout the tissue.

Description of Charcoal: Both dried and fresh charred tissue were similar. The tissues external to the cambium become very vesicular and partially solid in areas. While some cellular remains may be identified these tissues are

deteriorated largely beyond recognition (Figs. 1 to 3, Plate 34). The tissue of the xylem is, as would be expected from lignified tissues, preserved well. The parenchymatous rays are reduced to solid carbon (Figs. 1 to 2, Plate 34). The pith is often compressed by the formation of vesicular cavities (Fig. 2, Plate 34), but some intact tissue may survive (Fig. 5, Plate 34). The internal walls of cavities within the pith have impressions of storied parenchyma, (Fig. 6, Plate 34). The charcoal is black in colour dull in texture, hard and rather brittle.

DORONICUM GRANDIFLORUM

COMPOSITAE

Morphology: The organ under study is a wide somewhat dorsoventrally flattened stolon up to 2 cm across.

Anatomy: The stolon has an outer epidermis internal to which is an outer and inner ground tissue divided by a ring of vascular bundles. At the centre of the stolon is a region of very loosely arranged tissue made up of large parenchyma cells.

Epidermis: Single layer of tangentially flattened cells square in surface view. There is a thick cuticle.

Ground Tissue: Cells internal to the epidermis are highly tangentially flattened. These become gradually less flattened and more circular in transverse section away

from the epidermis. All of the cells are more or less circular in transverse section. Intercellular air spaces are large. Cells vary in size from 40 to 100 μm across becoming even larger towards the centre of the stolon where they may reach up to 130 μm across. Here they form a very loose arrangement with very large intercellular air spaces.

Vascular Tissue: Vascular bundles are collateral in arrangement. External to the phloem in each of the vascular bundles is a small group of fibres. Internal to the xylem is a horse shoe shaped group of fibres 2 to 4 cells thick. Both the phloem and the cambium form narrow elongated bands. The xylem, surrounded by fibres on three sides and the cambium on the fourth, is made up of between 35 to 45 thin walled polygonally shaped vessels in transverse section about 25 μm across and surrounded by xylem parenchyma. The vascular bundles are circular in transverse section 125 to 325 μm across.

Description of Charcoal: Tissue dried prior to charring and tissue charred from the fresh state were similar. The epidermis is lost but the ground tissue internal to it is preserved well as solid cells with clearly visible and discrete cell boundaries. There is a distinct difference between cells away from the epidermis (Fig. 5, Plate 35) and those adjacent to the epidermis (Fig. 6, Plate 35).

Cells may also be preserved slightly distorted (Fig. 10, Plate 34) or in a semi-solid state (Figs. 2 to 3, Plate 35). The tissue at the centre of the stolon breaks down to a highly deteriorated tissue (Fig. 1, Plate 35). The vascular tissue is deteriorated with the exception of the vessels of the xylem and some of the fibres, the remainder being reduced to solid carbon (Figs. 8 to 9, Plate 34). The charcoal is black in colour, hard and rather glassy.

INULA HELENIUM

COMPOSITAE

Morphology: The secondary root of this species is often unbranched thick and fleshy tapering over a length of up to 30 cm from a width of up to 4 cm. It has longitudinal ridges.

Anatomy: Internal to a narrow periderm is a region of parenchyma and phloem taking up to two fifths of the width of the root. Internal to a continuous cambium is a wide region of xylem composed largely of parenchyma. Secretory cavities occur in the xylem and the phloem but rarely in the outer parenchyma.

Periderm: This is made up of an outer layer of highly distorted and tangentially flattened cells internal to which is a single layer of thickened and more or less cubic cells.

Phloem/Parenchyma: Immediately internal to the periderm is a region of rounded but transversely elongated cells. These gradually become circular in transverse section towards the phloem. The cells are storied in longitudinal section. Internal to this is an entire ring of phloem adjacent to the cambium. Spherical secretory cavities approximately 150 μm across occur in the phloem and the parenchyma adjacent to it, but rarely close to the periderm.

Xylem: The cambium is continuous. Internal to the cambium are radially arranged rays of vessels. These are one vessel wide and may also contain fibres. The vessels are polygonal in transverse section, thick walled with circular lumina, 20 to 60 μm across. Secretory cavities up to 250 μm across occur throughout the tissue arranged in radial rows. The xylem parenchyma is storied but rather disorganised towards the centre of the root. There is a central core of vessels and fibres.

Description of Charcoal: Preservation of both dried and fresh charred tissues is good. The outer tissues become distorted by the formation of tangentially elongated vesicles (Fig. 7, Plate 35) though the cell walls are still easily identifiable. The tissue of the phloem and the cambium deteriorates to solid charcoal. The tissue of the xylem is preserved well so that the secretory cavities

(Fig. 8, Plate 35), vessels (Fig. 9, Plate 35) and parenchyma (Fig. 10, Plate 35) are easily identifiable. The charcoal is black in colour dull to glassy in texture, hard and brittle.

SAUSSUREA LAPPA

COMPOSITAE

Morphology: The secondary root of this species is typical of many fleshy tap roots of the Compositae being occasionally branched and tapering from the widest point of up to 4 cm at the root/shoot junction over a length of 20 to 30 cm.

Anatomy: The periderm is thick. Internal to this is an outer region of parenchyma and an inner region of phloem adjacent to the cambium. Internal to the cambium is a largely parenchymatous xylem and central parenchymatous pith.

Periderm: This is made up of several layers of cubic cork cells. The periderm may be very wide, distorted and contain within it both regions of parenchyma and secretory cavities.

Phloem/Parenchyma: Internal to the periderm and external to the cambium is a ground tissue of radially oriented rows of cells circular in transverse section and storied in longitudinal section as somewhat elongated cells. Intruding into this tissue and tapering away from the

cambium are narrow regions of phloem. These contain concentric rings of small fibre bundles. Throughout the ground tissue are secretory cavities with epithelial cells. The cavities are more or less spherical up to 150 μm across.

Xylem: The cambium is continuous. Internal to each of the radially oriented regions of phloem are similarly arranged rows of vessels running from the cambium almost to the centre of the root. Concentric rings of fibres occur throughout the tissue. Vessels are polygonal in transverse section, thin walled and up to 60 μm across. The xylem parenchyma is similar to that of the outer parenchyma except for that of the pith which is highly disorganised. Secretory cavities occur throughout the tissue.

Description of Charcoal: Dried and fresh charred tissues are similar. Despite a certain amount of solidification of certain tissues, the cambium and phloem, periderm and parts of the xylem parenchyma, preservation is good. The epithelial cells of the secretory cavities are also solidified, giving a smooth solid surface to the cavities (Fig. 5, Plate 36). Tissues of the outer parenchyma are preserved intact (Fig. 3, Plate 36) while tissue of the xylem parenchyma are deteriorated to solid charcoal (Fig. 6 to 7, Plate 36). This shows as

partially vesicular and compressed in longitudinal section. Vessels of the xylem are hard to identify in this tissue. The charcoal is black throughout, dull in texture hard and rather brittle.

SCORZONERA HISPANICA

COMPOSITAE

Morphology: The cultivated Scorzonera is a narrow unbranched fleshy secondary root tapering from a width of up to 3.5 cm at the transition zone over a length of up to 50 cm. The surface is rough.

Anatomy: Internal to a wide and thickened periderm is a layer of parenchyma containing laticifers and adjacent to the cambium, phloem. The xylem internal to the cambium consists of radially oriented rows of vessels and a parenchymatous ground tissue. Winton and Winton (1935) examined this species.

Periderm: 8 to 12 layers of highly thickened transversely flattened cells in rows.

Phloem/Parenchyma: Parenchyma immediately internal to the periderm is rounded but tangentially elongated. This progresses to a tissue made up of radially elongated cells closer to the cambium. Throughout this tissue are regions of phloem adjacent to the cambium and tapering towards the periderm. Throughout the ground tissue between the cambium and the periderm are articulated laticifers.

These form radially oriented rows within the phloem but are more random throughout the parenchyma closer to the periderm.

Xylem: The cambium is continuous. Internal to the cambium and opposite each of the regions of phloem are radially oriented rows of vessels. The rows radiate out from a solid core of vessels at the centre of the root but are not continuous and may contain wide regions of parenchyma. Vessels are polygonal in transverse section with circular lumina approximately 40 μm across. The xylem parenchyma cells are ovoid in transverse section, storied in longitudinal section and have large intercellular air spaces.

Description of Charcoal: While charcoal resulting from fresh tissue may be slightly more vesicular than that resulting from dried tissue, the results of charring are basically similar. The periderm becomes a more or less solid layer of carbon (Figs. 9 and 10, Plate 36). The outer tissues internal to the periderm including both phloem and laticifers becomes highly vesicular. Any remains of the laticifers or the phloem are indistinguishable amongst the general vesicular remains of the ground tissue. The outer tissues are tangentially oriented (Figs. 9 to 10, Plate 36 and Fig. 1, Plate 37), the inner tissues are radially oriented (Fig. 2, Plate

37). The cambium is deteriorated beyond recognition. The tissues of the xylem are deteriorated by the formation of radially oriented vesicles. These radiate out from the central axis and although many of the tissues are compressed some of the xylem parenchyma is preserved intact (Figs. 3 to 6, Plate 37). Individual vessels within the xylem are rarely identifiable as such. The charcoal is black to brown in colour, dull in texture and hard.

SCORZONERA JUDAICA

COMPOSITAE

Morphology: The perennating organ of this species is an almost spherical root tuber terminal on a much narrower root. The narrow root is up to 10 cm long and 5 to 10 mm wide. The tuber is 5 to 6 cm across with an irregular and uneven surface.

Anatomy: Despite its morphology the tuber has an anatomy similar to that of many other Compositae roots. Internal to a thickened periderm is a wide region of parenchyma and phloem. Internal to a discontinuous cambium are short radially oriented strands of vessels and a wide parenchymatous ground tissue.

Periderm: 5 to 8 layers of tangentially flattened and highly thickened cells in rows internal to which exist several layers of cork cells.

Phloem/ Parenchyma: Internal to the periderm is a layer of parenchyma containing articulated laticifers. The parenchyma is rectangular to cubic in shape with few intercellular air spaces. Adjacent to the cambium are narrow tapering regions of phloem intruding into the ground tissue.

Xylem: Internal to each of the discontinuous regions and opposite each of the regions of phloem are short radially oriented rows of vessels. These are no more than 2 to 3 vessels wide and 15 to 20 vessels long. Vessels are circular in transverse section with circular lumina 25 to 35 μm across. The ground tissue is similar to that external to the cambium. Occasional vessels occur throughout the xylem parenchyma.

Description of Charcoal: Tissue charred from the fresh state deteriorated to an extent beyond that which would allow survival during the normal taphonomic processes. Tissue charred from the dried state was well preserved but still very fragile and soft. Apart from some deterioration caused by breakdown of the tissues close to the periderm, primarily those containing laticifers, most of the cells were preserved intact. The tissue of the phloem also broke down to leave cavities although this was not the case in all specimens. Charred tissue of this species is shown in Figs. 7 to 10 on Plate 37 and Figs. 1

to 3 on Plate 38. The charcoal ranges from black to brown in colour and is very soft and friable.

SCORZONERA SCHWEINFURTHII

COMPOSITAE

Morphology: This is a similar plant to S. judaica, though the underground perennating organ in this case is a much longer and narrower tuber. This is almost cylindrical and attached to the aerial parts of the plant by a narrow root only 1 cm long. The tuber is up to 2 cm across and 10 cm long. The surface is again irregular and uneven.

Anatomy: The anatomy of this species is basically similar to that of the previous species the only difference being in the relative widths of the parenchymatous ground tissue external to and internal to the cambium. In S. judaica the tissue internal to the cambium is 5 to 6 times the width of the tissue external to the cambium. In S. schweinfurthii the ground tissue external to and internal to the cambium is equal and about the same width as that of the outer tissues of S. judaica.

Description of Charcoal: The tissue resulting from the charring of dried tissue is again the only tissue that would usually survive normal taphonomic processes. Dried charred tissues are preserved well, again with the exception of the laticifer bearing tissues and the phloem (Figs. 5 and 6, Plate 38). Tissues internal to the

cambium are generally preserved intact with the exception of some cells around individual vessels of the xylem (Figs. 7 to 10, Plate 38). The charcoal is black to brown in colour dull in texture and extremely soft and fragile.

TARAXACUM OFFICINALE

COMPOSITAE

Morphology: The secondary root is a fleshy often branched structure tapering from a width of up to 2 to 3 cm at the transition zone over a length of up to 20 cm. The surface is transversely wrinkled.

Anatomy: Internal to a narrow periderm is a wide region of parenchyma containing concentric rings of phloem. The central fifth of the root is a solid core of xylem vessels with small amounts of xylem parenchyma.

Periderm: Narrow layer of variously thickened tangentially flattened cells.

Phloem/Parenchyma: The outer two fifths of the root is made up of a parenchymatous ground tissue. It is tangentially elongated immediately internal to the periderm becoming radially elongated further towards the tissue of the phloem. Many of the cells near the periderm are in the form of chains derived from the periclinal division of tangentially elongated cells. The central cells of such chains are square or rectangular in transverse section, the outer cells being rounded. The

first of up to nine concentric rings of phloem lies internal to the outer two fifths of the radius of the root. The outer rings are formed from discrete bundles of phloem whereas the inner rings are formed from complete rings of phloem. Parenchyma between the rings is radially oriented and rectangular in transverse section. All the parenchyma external to the cambium is storied in longitudinal section. Between the innermost ring of phloem and the xylem is a narrow cambium.

Xylem: Internal to the cambium is a solid core of xylem made up of many vessels either singly or in groups of up to 5. There is a ground tissue of xylem parenchyma. Vessels are polygonal in transverse section with rounded lumina up to 40 μm across with the exception of the outermost ring of vessels which may reach up to 70 μm across and occasional lenses of vessel groups which may also reach over 40 μm across.

Description of Charcoal: Charcoal derived from both fresh and dried charred tissues were similar. The periderm, outer parenchyma, phloem and phloem parenchyma are preserved well, but suffer deterioration caused by the formation of tangentially oriented cavities caused by a combination of both tension fracturing and vesicle formation, (Figs. 1 to 3, Plate 39). The cambium deteriorates to a solid ring of carbon adjacent to the

outermost ring of vessels of the xylem, (Fig. 4, Plate 39). The xylem parenchyma deteriorates to solid carbon creating a very solid central core, (Figs. 4 to 6, Plate 39). The charcoal is black to brown in colour. The outer tissues are dull in texture rather soft and flaky. The inner core of xylem is glassy and much harder.

TRAGOPOGON PRATENSIS

COMPOSITAE

Morphology: This is a narrow, occasionally branched fleshy secondary root similar to that of Cichorium intybus. It tapers from a width of 2 to 2.5 cm over a length of up to 25 cm.

Anatomy: The roots of Tragopogon pratensis and Tragopogon porrifolius, the cultivated salsify are anatomically interesting in that they retain the primary tissues of the cortex and endodermis while still undergoing secondary growth. A periderm is therefore derived from the parenchyma of the cortex rather than from the tissue of the pericycle. The narrow cortex persists and is divided from the phloem and phloem parenchyma by the endodermis. A narrow but continuous cambium then separates the phloem from a rather woody xylem. There is a central parenchymatous pith. Winton and Winton (1935) and Havis (1935) have examined Tragopogon porrifolius.

Periderm and Cortex: The periderm consists of 2 to 3 layers of variously thickened and partially distorted cells, more or less cubic in shape. Internal to this are 3 to 4 layers of tangentially oriented chains of 2 to 5 cells with large intercellular air spaces between them. These are formed by the periclinal division of tangentially elongated cells in a similar way to the outer ground tissue of Taraxacum officinale. These cells persist through to the endodermis.

Endodermis: Single layer of rectangular to cubic cells 30 μm across. There is a prominent casparian strip.

Phloem/Parenchym: An outer region of tangentially elongated cells gives way to isodiametric cells large intercellular air spaces. Intruding into this are regions of phloem adjacent to the cambium and tapering towards the endodermis.

Xylem: The xylem lies internal to a narrow but continuous cambium. It is made up of an outer ring of fibres and vessels. The vessels are thin walled, circular in transverse section and between 30 to 60 μm across. The fibrous ground tissue gives way to a parenchymatous ground tissue towards the centre of the root. Vessel size increases towards the fibre/parenchymatous ground tissue boundary both from the cambium and from the central axis.

Pith: Parenchymatous, containing relatively few vessels. Cells are circular in transverse section 20 μm across and

storied in longitudinal section where they are elongated up to 125 μm .

Description of Charcoal: All of the outer tissues are compressed into a narrow and fragile outer region of carbon (figs. 1 and 3, Plate 40). The tissue of the xylem is preserved intact both vessels, fibres and parenchyma (Figs. 1 and 4 to 7, Plate 40). The tissue of the pith is deteriorated to a flaky mass of broken cell walls (Fig. 2, Plate 40). The charcoal is black throughout, dull to glassy in texture and rather brittle.

6.3.2 Monocotyledons

BUTOMUS UMBELLATUS

BUTOMACEAE

Morphology: Shoots grow from a narrow rhizome, slightly dorsoventrally flattened, with fibrous roots emerging along the length of the lower side. The rhizome is approximately 1 to 2 cm across and grows reasonably straight (Lieu 1979). Wilder (1974) tackled the problem of whether the rhizome was monopodial or sympodial.

Anatomy: Internal to a narrow epidermis is an aerenchymatous cortex separated from a central mass of ground tissue by an endodermal like layer of thickened cells. Vascular bundles run apparently randomly through the central mass of ground tissue.

Epidermis: Single layer of unthickened cells, cubic in shape.

Cortex: Internal to the epidermis are 3 to 4 layers of isodiametric cells. This gives way to a narrow layer of aerenchyma made up of plates of isodiametric cells 15 to 30 μm across. Some of these have a secretory function and many contain cubic rectangular or rod shaped crystals. The cortex is internally delimited by a region of thickened cells more or less isodiametric and angular in shape.

Pith: This is made up of spherical cells 35 to 40 μm

across or cells circular in transverse section and elongated up to 65 μm . Intracellular air spaces are large.

Vascular Tissue: Vascular bundles run apparently randomly through the pith. These vary in both size and organization. Bundles are often circular in transverse section with an amphi-cribal concentric. Fibre caps lie on the outer side of small bundles and on both the inner and outer side on large bundles. The fibre caps vary in size from only a few fibres to fibre masses 4 by 20 cells across. A few of the bundles have no fibre caps. The xylem is made up of only a few tracheids embedded in a matrix of phloem. The smaller bundles have only 1 to 2 trachary elements and a few have none at all. Some bundles are irregular in shape often elongated in transverse section composed of tracheids and fibres embedded in a phloem matrix. Stant (1967) examined this species.

Description of Charcoal: Both dried and fresh charred tissues are similar. All the tissues external to the outer tissues of the pith are turned to ash and so do not survive in any recognisable form. The tissue of the pith is preserved well, individual cells of the ground tissue being easily discernable. These become very thick walled on charring with thick internal cross walls, (Figs. 1 to

3, Plate 41). The vascular tissue with the exception of the xylem, deteriorates to solid or semi-solid carbon (Figs. 9 to 10). Occasional vesicles are large and elongated along the long axis of the rhizome. The internal walls show the longitudinal pattern of the ground tissue impressed upon them (Fig. 4, Plate 41). The charcoal is black to brown in colour, dull to glassy in texture and rather hard and brittle.

ALISMA PLANTAGO-AQUATICA

ALISMATACEAE

ALISMA LANCEOLATUM

Morphology: In terms of the morphology of the caudex type rootstock these two species are similar. The caudex is almost spherical, between 2 and 5 cm across. Narrow fleshy roots emerge from all over its surface. Emerging from the upper surface is a short pointed and truncated crown.

Anatomy: Again the anatomy of the caudex of these two species is similar. Stant (1964) and Tomlinson (1969) have examined both of these species. Internal to a narrow epidermis is a thin aerenchymatous cortex separated from a wide aerenchymatous pith by a thickened layer of parenchyma. Vascular bundles run apparently randomly through the pith.

Epidermis: A single layer of radially elongated

unthickened cells.

Cortex: Immediately internal to the epidermis is an aerenchymatous cortex made up of plates of stellate parenchyma. Small intercellular air-spaces occur within the plates and large intercellular air-spaces between the plates. The latter are up to 170 μm across. The internal boundary of the cortex is delimited by a region of cubic to irregularly shaped parenchyma cells.

Pith: Internal to the cubic cells delimiting the internal boundary of the cortex are several layers of irregularly shaped parenchyma cells giving way to an aerenchymatous pith. This is made up of chains of spherical cells 25 to 35 μm across. Running apparently randomly through the pith are vascular bundles and a network of latex ducts. The latter are circular in transverse section 50 μm across and lined with epithelial cells.

Vascular Tissue: Vascular bundles vary in size, shape and organization. Some are amphivasal concentric in arrangement, but never having an entire ring of xylem. Others are circular in transverse section with trachery elements embedded in a matrix of phloem. Many bundles are irregular in shape, composed of a confused mass of both phloem and xylem. The trachary elements are thin walled and polygonal in transverse section 10 to 15 μm across.

Description of Charcoal: Both dried and fresh charred

tissues from both Alisma plantago-aquatica and Alisma lanceolatum were similar. Only A. plantago-aquatica is illustrated. The tissues external to the outer tissues of the pith turned to ash and do not survive. The tissue of the pith is well preserved though many of the aerenchyma cells are compressed against the internal walls of large intercellular air spaces (Figs. 5 to 7, Plate 41). The vascular tissue is easily identifiable as solid tracts of carbon with few of the phloem tissues being preserved intact. The tissue of the xylem is easily definable amongst the deteriorated remains of the other tissues within the vascular bundle (Figs. 8 to 10, Plate 41 and Fig. 1, Plate 42). The charcoal is black to brown in colour, very soft and rather fragile.

SAGITTARIA SAGITTIFOLIA

ALISMATACEAE

Morphology: The organ under study is a tuber occurring terminally on a stolon. It is ovoid in shape, the proximal end being attached to the stolon and the distal end terminating in a bud. The tuber is up to 4 cm across and 8 cm long and covered with scale leaves. This is described by Arber (1920).

Anatomy: Internal to an epidermis there may or may not be present a narrow region of aerenchyma. If present it gradually becomes solid parenchyma 4 to 5 cell layers into

the tuber. If no aerenchyma is present solid parenchyma lies immediately internal to the epidermis. Running through the parenchymatous ground tissue of the tuber is a network of latex ducts and vascular bundles. Winton and Winton (1935) have examined this species.

Epidermis: Single layer of cubic to rectangular cells.

Aerenchyma: If present it is then formed by anticlinally oriented chains of spherical cells connected by short periclinally oriented chains. Inter cellular air spaces are up to 130 μm across.

Parenchyma: The ground tissue is made up of more or less spherical cells 70 to 125 μm across. Inter cellular air spaces are large. A system of ducts lined with epithelial cells runs through the tissue. These are circular in transverse section and between 40 and 170 μm across.

Vascular Tissue: Vascular bundles are circular in transverse section composed largely of phloem with up to 4 trachery elements embedded within the tissue. Some bundles are composed only of phloem. Trachery elements are polygonal in transverse section, thin walled approximately 8 μm across. Bundles range from 50 to 180 μm across.

Description of Charcoal: Dried and fresh charred tissues are similar. Preservation is poor, the majority of the tissues becoming vesicular and partially solid. Irregularly shaped vesicles form randomly throughout the

charred tissue (Fig. 5, Plate 42). The inside walls of these have the impressions of cells upon them (Fig. 7, Plate 42). Other regions of the tissue become solid or may be preserved intact (Figs. 3 to 4 and 8, Plate 42). The charcoal is black throughout, rather shiny and very soft.

ARRHENATHERUM ELATIUS ssp. BULBOSUM

GRAMINEAE

Morphology: Typical of many of the Gramineae and exemplified by both this and the following species is the swollen lower internode of an upright axis. Small tubers are formed by the swelling of an internode close to the base of the vertical axis. In Arrhenatherum elatius ssp. bulbosus these are up to 7 mm across and 4 cm long. The surface is smooth.

Anatomy: Internal to a thickened epidermis is a parenchymatous ground tissue containing a ring of vascular bundles close to the epidermis. The centre of the pith is partially broken down.

Epidermis: A single layer of highly thickened rectangular cells 20 μ m across.

Ground Tissue: Consists of polygonal cells with very small intercellular air spaces. Immediately internal to the epidermis these are 20 to 25 μ m across, adjacent to the ring of vascular bundles approximately 50 μ m across. The

innermost cells are 85 to 90 μm across. Parenchyma cells between the vascular bundles tend to be radially elongated.

Vascular Tissue: Vascular bundles form a ring about one fifth of the way across the radius of the tuber. Each bundle is surrounded by a sheath of fibres 1 to 4 cells deep. A narrow band of fibres separates the phloem (external) from the xylem (internal). The xylem comprises of two large laterally placed vessels adjacent to the parenchyma at the centre of the xylem tissue. Vessels are circular in transverse section, thick walled and 25 μm across. Small bundles have less xylem tissue, the smallest bundles being composed of phloem only. The vascular ring is two to three bundles deep, each bundle being 3 to 6 parenchyma cells apart.

Description of Charcoal: Tissues charred from the fresh state produced a very thin and fragile shell of deteriorated tissue that would not normally survive the usual taphonomic processes. Tissues charred from the dried state produce a reasonable well preserved charcoal. The thickened epidermis and outer cell layers compress to form a solid layer of charcoal (Fig. 10, Plate 42). Tissues internal to this are preserved well with the exception of the innermost ground tissue which breaks down to form a cavity (Fig. 9, Plate 42), and the phloem which

deteriorates to a solid carbon mass within the vascular bundle. The ground tissue is to a certain extent artificially thickened but still easily recognisable as parenchyma (Fig. 3, Plate 43). Tissues at either end of the tuber close to the nodes, rather than at the centre of the internode, have a slightly different organization. Vascular bundles, instead of being restricted to an outer ring are apparently randomly placed throughout the tissue. There is no breakdown of the central ground tissue (Figs. 1 to 2 and 6, Plate 43). The charcoal is black throughout, the external surface is shiny while the internal tissues are dull to glassy. The charcoal is soft and brittle.

HORDEUM BULBOSUM

GRAMINEAE

Morphology: This is similar to that of Arrhenatherum elatius ssp. bulbosus - a swollen lower internode of a vertical stem. The tuber here is approximately 1.5 cm long and 5 to 6 cm across.

Anatomy: Internal to a narrow thickened epidermis is an entire ring of fibres. Internal to this is a ring of small vascular bundles. The parenchymatous ground tissue internal to this has larger vascular bundles running through it.

Epidermis: A single layer of more or less cubic cells

thickened on their outer tangential walls.

Ground Tissue: Internal to the epidermis is a continuous ring of fibres 2 to 4 cells deep. The ground tissue internal to this and throughout the tuber is composed of polygonally shaped parenchyma cells 20 to 25 μm across close to the epidermis increasing in size to 50 to 60 μm across at the centre of the pith.

Vascular Tissue: A ring of small vascular bundles occurs just internal to the fibre ring. These are circular in transverse section 50 to 60 μm across. Each have a sheath of fibres one cell thick internal to which is an external region of phloem and internal xylem. All bundles however small contain both xylem and phloem. Larger vascular bundles occur in the pith. These are similar in arrangement but may be ovoid in shape.

Description of Charcoal: Tissue charred from the fresh state resulted in thin fragile fragments of charcoal that would normally survive the usual post preservation taphonomic processes. Tissue derived from dried material of this species is preserved well with the survival of the majority of the cells (Figs. 7 to 8, Plate 43). Some of the ground tissue is reduced to solid carbon (Fig. 8, Plate 43), though most is preserved intact. The tissue of the phloem deteriorated in every case to solid carbon, but otherwise the vascular tissues are preserved intact, (Fig.

9, Plate 43 and Fig. 3, Plate 44). The charcoal is black throughout with a shiny outer surface and a dull to glassy internal tissue. The charcoal is soft and brittle.

CYPERUS ESCULENTUS

CYPERACEAE

Morphology: The specimens observed were the cultivated 'Tiger Nuts' commercially sold in Britain. These are stem tubers formed as terminal swellings on a rhizomatous stem system. The tubers are ovoid, up to 2 cm long and 1 cm in diameter. They are multinodal and terminate in 2 to 3 dormant buds internal to reduced scale leaves. Fibrous roots occur at nodes.

Anatomy: Internal to a narrow epidermis is a region of highly thickened cells and internal to this and throughout the tuber a parenchymatous ground tissue. This is divided into an outer cortex and inner pith by a narrow endodermis. Vascular bundles are restricted to a narrow region of the pith close to the endodermis. Stoller, Nema and Bhan (1972) have examined this species.

Epidermis: This is very thin, mostly ruptured and identifiable in most cases only by the remains of cell walls.

Ground Tissue: Immediately internal to the epidermis is a region of highly thickened radially elongated cells. This region is approximately 90 μm across made up of three to

six cell layers. The parenchymatous ground tissue of the cortex and the pith are similar being composed of polygonal cells more or less isodiametric, 40 μ m across.

Endodermis: Lying one third of the way across the radius of the tuber the endodermis consists of 1 to 2 layers of tangentially flattened cells 30 to 35 μ m long, and 15 μ m across. These are unthickened.

Vascular Tissue: Vascular bundles run directly adjacent to or near to the internal endodermal wall. These are irregular in shape 80 to 85 μ m across with an amphivasal concentric arrangement. The ring of xylem elements is up to two cells thick but rarely complete.

Description of Charcoal: Charred fresh and dried tissues of this species are similar. Most tissues are intact on charring with the exception of certain parts of the vascular tissue and the epidermis. The epidermis is lost completely (Fig. 6, Plate 44 and Fig. 1, Plate 45). Upon the surface of the tuber may be seen rhizome detachment scars (Fig. 4, Plate 44), root scars (Fig. 5, Plate 44), and terminal bud scars (Fig. 7, Plate 44). The latter in section reveal bud primordia internal to scale leaves, (Figs. 8 to 9, Plate 44). The external layer of thickened cells is the outermost cell layer to survive, (Fig. 1, Plate 45). Several states of preservation of the ground tissue were observed, (Figs. 2 and 4 to 7, Plate 45). The

endodermis is reduced to solid carbon as is all the vascular tissue with the exception of the xylem trachery elements. The charcoal is black throughout, dull and hard.

CYPERUS LONGUS

CYPERACEAE

Morphology: A network of aerial shoots is connected by a narrow multinodal system of rhizomes. This is homogeneous along its length approximately 8 mm across. Internodes are between 1 and 6 cm apart.

Anatomy: Organization of tissues is similar to that of C. esculentus, the only differences being in the vascular tissue. Sclerenchymatous tissue may be associated with the endodermis.

Vascular Tissue: Vascular bundles occur throughout the pith and the cortex though in the latter they are small. Bundles in the pith are about 90 μm across. Both are amphivasal concentric in arrangement. Each bundle has an outer sheath of fibres 1 to 2 cells across, an entire ring of xylem and an inner core of phloem. Vessels are elongated in transverse section in an axis radiating away from the centre of the bundle. Vessels are thin walled and approximately 25 μm across.

Description of Charcoal: Preservation of both fresh and

dried tissues was similar. The majority of tissues are preserved intact with the exception of the phloem. Due to the high concentration of vascular bundles throughout the pith the deterioration of the phloem leaving cavities causes some distortion of this tissue (Fig. 10, Plate 45 and Figs. 1 to 2, Plate 46). The cortex and the endodermis are preserved intact (Figs. 8 to 9, Plate 45). The charcoal is black throughout, dull and rather hard becoming glassy in places.

CYPERUS ROTUNDUS

CYPERACEAE

Morphology: Both Davis (1942) and recent observations by Gordon Hillman (Hillman, Madyeska and Hather: 1988) have shown that the morphology of Cyperus rotundus varies over a cline between two extremes of habitat. Plants growing in well drained soil tend to grow in a manner similar to that previously described for C. esculentus. That is to say producing multinodal ovoid tubers on a much narrower system of rhizomes. It is important to note that tubers of C. rotundus are not necessarily terminal on a rhizome. Tubers growing in this habitat are similar in size to those of C. esculentus. Plants growing in a waterlogged habitat, on the edges of rivers, lakes etc. with a system of rhizomes internal to the water level differ in that the distinction between rhizome and tuber is much less

heterogenous. Rhizomes are swollen and tubers appear as only slightly more swollen regions along these. The whole rhizome-tuber system is far more irregular. Intermediate forms occur at intermediate habitat types.

Anatomy: While the basic organization of tissues is similar in both morphological forms there are distinct anatomical differences between the two. In order to explain these fully the non-waterlogged tubers will be described before contrasting them with the waterlogged tubers.

Non-waterlogged: Internal to a narrow ruptured epidermis lie longitudinally oriented ridges of stone cells. The parenchymatous ground tissue is divided by a slightly thickened endodermal region into a cortex and pith. Vascular bundles are distributed apparently randomly throughout the pith.

Epidermis and Stone Cell Layer: The epidermis is narrow and largely ruptured. Internal to the epidermis lie longitudinally oriented ridges of stone cells, these are not connected to each other but are adjacent to a distinct lower continuous layer of stone cells.

Ground Tissue: The parenchymatous ground tissue of the cortex and pith is similar, being made up of polygonal cells approximately 40 μm across. Inter cellular air spaces are small and few.

Endodermis: 2 to 3 layers of tangentially flattened cells

each 5 to 10 μm across. These are slightly thickened.

Vascular Tissue: Vascular bundles are distributed randomly throughout the pith. These are circular in transverse section 80 to 160 μm across. They are amphivasal concentric in arrangement with, in most cases, a near complete ring of xylem 1 to 2 cells deep. Trachery elements are polygonal in transverse section 15 to 20 μm across and thick walled with circular lumina.

Waterlogged: The arrangement of tissues is similar though two important differences are apparent. The epidermis is intact and the distinct arrangement of stone cells is lacking. Internal to the epidermis are 3 to 4 layers of slightly thickened polygonal cells with small longitudinal oriented bundles of fibres lying close to the epidermis. The endodermis is similar to that of non-waterlogged types but only one cell thick. Vascular bundles are similar in arrangement but only 50 to 80 μm across these are greater in number and are apparently distributed less randomly. This is a reflection on the less truncated nature of the nodes and internodes of this morphological form.

The rhizome anatomy of the non-waterlogged morphological form is reflected in the transverse section of tissues left by the detachment of the rhizome. These scars show a transition from the concentric bundles of the tuber to the collateral bundles of the rhizomes. Collateral bundles

have an external region of phloem and internal xylem made up to two large laterally placed metaxylem elements at the xylem/phloem junction. At the point of the rhizome attachment to the tuber each vascular bundle has a wide fibre sheath. No such transition in vascular bundle organization from the concentric bundles of the tuber was observed in the waterlogged morphological form.

Description of Charcoal: Fresh and dried tissues were similar. Both morphological types were experimentally charred: the only resulting differences reflecting the relative anatomical and morphological forms. The outermost layers whether lignified or not turned to ash. The external surviving layers of charred tubers is the outermost parenchyma of the cortex (Fig. 8, Plate 46). However in some cases the central vascular tract of scale leaf that surround the tuber persist, (Figs. 6 and 7, Plate 46). All tissues internal to the outermost tissues of the cortex are preserved more or less intact. The ground tissue may become vesicular (Fig. 9, Plate 46), thick walled, but otherwise well preserved (Fig. 2, Plate 47) or become solid (Fig. 3, Plate 47). Vascular tissue, shown here to be transitional between concentric and collateral (Fig. 10, Plate 46 and Fig. 1, Plate 47) is well preserved with the exception of the phloem which deteriorates to form a cavity. This is also noticeable in

longitudinal fracture planes (Figs. 4 to 6 and 8, Plate 47). The tissue of the xylem may be well preserved (Fig. 7, Plate 47). The charcoal is black throughout, dull in texture and hard.

SCHOENOPLECTUS TABERNAEMONTANI

CYPERACEAE

Morphology: Shoots arise from a thick, fleshy, creeping rhizome up to 4 cm in diameter and circular in transverse section. Fibrous roots emerge mainly from the lower surface. Shoots occur at nodes which are between 3 and 10 cm apart. Scale leaves occur at all nodes.

Anatomy: Internal to a narrow epidermis is an outer fibrous region of the cortex, internal to which is a much wider aerenchymatous inner cortex. An endodermal structure separates the cortex from an aerenchymatous pith. Vascular bundles occur mainly internal to the endodermis.

Epidermis: Narrow layer of rectangular slightly rounded cells up to 16 μm across.

Cortex: Immediately internal to the epidermis is a continuous layer of thickened cells 40 μm across. Within this layer are bundles of fibres 4 to 8 cells across. A narrow region of parenchyma internal to this gives way to aerenchyma made up of plates of spherical to longitudinally elongated cells 30 to 40 μm across.

Intercellular air spaces between chains are up to 125 μm across.

Endodermis and Pith: The endodermis is formed by an outer ring of fibres and an inner ring of parenchyma cells, square in transverse section but longitudinally elongated. The ground tissue of the pith is similar to that of the inner cortex.

Vascular Tissue: A few small vascular bundles occur in the cortex although the majority occur in the pith. Vascular bundles adjacent to the internal wall of the endodermis appear flattened against it, the vascular tissues being wider spread than in bundles embedded in the aerenchyma away from the endodermis. The concentration of bundles decreases towards the centre of the pith. The vascular bundles are collateral, having a fibre sheath one cell thick at the phloem and up to eight cells thick at the xylem. Vessels are approximately 25 μm across, polygonal in transverse section and thin walled. Between 3 and 6 vessels form an arch surrounding the phloem on three sides. Internal to this is a small amount of xylem parenchyma containing a few small vessels.

Description of Charcoal: Due to the aerenchymatous nature of the tissues of this species only rhizomes dried prior to charring were preserved in a state that would survive the normal taphonomic processes. Even so, preservation

here was poor. The ground tissue becomes compressed so that the large aerenchymatous air spaces appear as cell lumina, the 'cell walls' being made up of flattened cell plates. The impressions of cell walls are visible upon these (Figs. 9 to 10, Plate 47). Vascular tissue is preserved well with the exception of the phloem which is deteriorated to solid carbon. All the tissues of the xylem are preserved intact (fig.1, Plate 48). The charcoal is black throughout, dull in texture soft and rather brittle.

SCIRPUS MARITIMUS

CYPERACEAE

Morphology: Shoots arise from a complex system of swollen stem bases connected by thick rhizomes which may terminate in ovoid tubers. The swollen stem bases are multinodal vertical stem tissue and rounded. Each may be termed a caudex. These are 2 to 4 cm across. Rhizomes are cylindrical 7 mm across tubers ovoid 1 to 2 cm by 3 to 4 cm. Tubers are transitional organs that may become swollen stem bases the following season.

Anatomy: Despite the obvious morphological differences the anatomy of the caudex, rhizome and tuber are similar. Internal to a narrow epidermis is a fibrous outer cortex and a much wider aerenchymatous inner cortex. A highly thickened endodermal structure separates the cortex from a

solid parenchymatous pith through which run apparently more or less randomly placed vascular bundles.

Epidermis: A narrow, single layer of rectangular unthickened cells.

Cortex: Immediately internal to the epidermis is a narrow layer of fibres 3 to 4 cells thick. Internal to this are 5 to 6 layers of spherical cells. These give way to an aerenchymatous ground tissue made up of spherical cells held away from each other by up to 5 or 6 arm-like extensions. At the junction between the parenchymatous and aerenchymatous tissues of the cortex is a ring of fibre bundles, each approximately 35 μm across.

Endodermis: Internal to a continuous outer layer of fibres 2 to 3 cells deep is a layer of parenchyma square in transverse section and longitudinally elongated 10 to 15 μm across.

Pith: The ground tissue of the pith is composed of isodiametrically polygonal cells 30 to 35 μm across. Inter cellular air spaces are few and small.

Vascular Tissue: Vascular bundles vary in shape but are generally ovoid and have a thick fibre sheath. This is wider at the xylem pole than at the phloem pole. Commonly the xylem forms an arch of 3 to 6 vessels surrounding the phloem on three sides; however often a band of fibres lies between the xylem and the phloem. Xylem parenchyma is often associated with the vessels forming a region between

the vessels arch and the fibre sheath. Where nodes are close together such as in the caudex or in the tuber, bundles tend to be more randomly placed than where nodes are further apart, such as in the rhizome.

Description of Charcoal: Dried and fresh charred tissues were similar. All tissues external to the fibre layer of the endodermal structure do not survive. With the exception of occasional cavities caused by tension fractures the ground tissue is preserved intact (Figs. 4 and 5, Plate 48). Vascular tissue, with the exception of the phloem is preserved intact (Figs. 6 to 8, Plate 48). This is shown well on rhizome detachment scars on tubers and swollen stem bases where there is a concentration of vascular tissue in a narrow area (Figs. 7 and 8, Plate 48). Here cavities are visible where the tissue of the phloem has broken down. The charcoal is black throughout, dull hard and brittle.

TYPHA LATIFOLIA

TYPHACEAE

TYPHA ANGUSTIFOLIA

Morphology: Shoots occur along the length of cylindrical rhizomes with widely spaced internodes. Large swollen regions up to 6 cm across occur where shoots appear. T. latifolia has rhizomes up to 3 cm across, T. angustifolia

has rhizomes never larger than 2 cm across. Otherwise in terms of rhizome morphology the two species are similar.

Anatomy: Rhizomes and swollen stem bases are similar anatomically having a narrow epidermis below which is a parenchymatous outer cortex and aerenchymatous inner cortex. Internal to an unthickened endodermal structure is an aerenchymatous pith in T. latifolia and parenchymatous pith in T. angustifolia. Vascular bundles are contained within the pith. Ervin and Evert (1970) examined T. latifolia.

Epidermis: Single narrow layer of unthickened cubic cells 15 to 20 μm across.

Cortex: Immediately internal to the epidermis is a region of parenchyma made up of 9 to 10 layers of polygonal cells 40 to 50 μm across. A much wider inner cortex is composed of aerenchyma. This is made up of cells that are long and thin in transverse section, forming chains around polygonal intercellular air spaces 80 to 150 μm across. In longitudinal section the chains are storied and the air spaces elongated up to 400 μm . Throughout the aerenchyma, at the corners of the polygonally cylindrical air spaces are a variety of structures; large somewhat thickened cells, fibre and vascular bundles with parenchymatous sheaths. The vascular bundles contain either phloem and xylem or only xylem. Some of these may have fibre caps at each pole. The parenchymatous sheaths contain rod shaped

crystals.

Endodermis: Single layer of thickened cells rectangular in shape internal to which are several layers of tangentially flattened cells.

Pith: The ground tissue of the pith is aerenchymatous in T. latifolia made up of chains of more or less spherical cells. Intercellular air spaces are 40 to 125 μm across. In T. angustifolia the ground tissue is made up of solid parenchyma. The cells are polygonal in shape and intercellular air spaces are small.

Vascular Tissue: Apart from the few vascular bundles in the cortex the majority of the vascular tissue is within the pith. In both species this is similar in both vascular bundle arrangement and in the organization of the tissues within the bundles. Vascular tissue in the swollen stem bases is highly disorganized compared with that of the rhizomes. Bundles are ovoid in shape and radially elongated with the exception of those adjacent to the endodermis. these are tangentially elongated. A thick fibre cap lies internal to the xylem. The vascular tissue is collateral in arrangement the xylem consisting of 3 to 4 vessels 45 to 50 μm across, and a small amount of parenchyma. The phloem forms a region, circular in transverse section with sieve tubes 25 to 30 μm across. A sheath of parenchyma surrounds the phloem.

Description of Charcoal: All tissues external to the

endodermal structure are destroyed on charring. Tissues charred from the dried state are preserved intact internal to the endodermis with the exception of the tissue of the phloem. This breaks down to form a cavity in each of the vascular bundles, (Fig. 10, Plate 48 and Fig. 1, Plate 49). Tissues charred from the fresh state become far more vesicular with greater deterioration of the vascular and ground tissues, (figs. 2 to 3, and 5 to 8, Plate 49). In both cases the external surface of the outer tissues of charred fragments bear the remains of the outer epidermal layer (fig. 4, Plate 49). The charcoal is black throughout, hard and dull.

SPARGANIUM ERECTUM

SPARGANIACEAE

Morphology: Similar to Scirpus maritimus this is a complex of swollen stem bases or caudexes and rhizomes. Rhizomes are cylindrical 1 to 2 cm across and stem bases 2 to 4 cm across. Fibrous roots occur at nodes.

Anatomy: This is similar throughout the stem base and rhizome complex whether vertically or horizontally oriented. Internal to a narrow unthickened epidermis is a parenchymatous outer cortex and aerenchymatous inner cortex. Internal to an endodermal structure internal to the cortex is a pith of solid parenchymatous tissue.

Epidermis: A single layer of rectangular cells 15 to 20 μm

across.

Cortex: Immediately internal to the epidermis is a region of parenchyma both tangentially and longitudinally elongated. These cells decrease in size away from the epidermis from 75 μm across to 35 to 40 μm across. The cells then forming an aerenchymatous tissue. The inner and outer cortex are more or less equal in width, there is no clear junction between the two. Throughout the tissue run fibre bundles some containing a core of phloem.

A few of the bundles contain both xylem and phloem.

Endodermis: Several layers of cells decreasing in size towards the pith. The layer is unthickened and narrow.

Pith: Solid more or less isodiametric polygonal cells with the exception of those adjacent to the vascular bundles. These are elongated in an axis radiating out from the centre of each bundle. Cells are 50 μm across. Those elongated adjacent to the vascular bundles are up to 80 μm across.

Vascular Tissue: Vascular bundles situated in the pith are circular to ovoid in transverse section, 100 to 275 μm across. The bundles are collateral, made up of irregular external masses of phloem and internal masses of xylem surrounded by a parenchymatous sheath. Fibre caps may or may not lie at the xylem and or the phloem poles. Vessels are circular in transverse section thin walled and 20 to 30 μm across.

Description of Charcoal: Both charred fresh and dried tissues are similar. The outer tissues of the cortex are compressed to a narrow band of flattened cell walls. The endodermis is deteriorated to a solid narrow layer of carbon (Figs. 9 to 10, Plate 49). The tissue of the pith remains intact though the cell walls are somewhat thickened (Figs. 1 to 2 and 5, Plate 50). Vascular tissue may be deteriorated so that the vessels appear as gaps in a tract of solid carbon (Fig. 3, Plate 50) or so that most of the tissue is preserved well (Fig 4, Plate 50). The charcoal is black throughout dull to glassy, hard and rather brittle.

ALPINIA GALANGA

ZINGIBERACEAE

Morphology: Typical of Zingiberaceae rhizomes this is a rather stout regularly branching structure. Each internode is similar in length and width at approximately 2 to 4 cm. Unlike Zingiber officinale the mid-internodal region tends to be slightly wider than the node. Bell (1979) and Tomlinson (1969) have examined branching patterns in this species.

Anatomy: Internal to a narrow epidermis is an outer cortex and inner pith, more or less equal in width. These are separated by an indistinct endodermal region. Vascular bundles occur in both the cortex and the pith.

Epidermis: A single layer of rectangular cells 25 to 30 μm across.

Ground Tissue: Parenchyma cells, polygonal and isodiametric in transverse section and longitudinally elongated. Cells immediately internal to the epidermis are 80 μm across and 200 μm long. 8 to 9 cell layers internal to this the cells gradually become smaller at 50 μm across and 100 μm long. They remain at this size throughout the rhizome.

Endodermis: Separating the cortex and the pith is an indistinct endodermal layer made up of a single layer of rectangular, tangentially flattened and unthickened cells.

Vascular Tissue: Vascular bundles occur in both the pith and the cortex although are larger and more highly concentrated in the latter. Cortical bundles range from 80 to 140 μm across: pith bundles range from 130 to 274 μm across. Tissue arrangement of the bundles varies but generally collaterally arranged with a thick fibre sheath at the xylem pole narrowing or missing at the phloem pole. The xylem is made up of between 1 and 7 vessels. Xylem parenchyma surrounds the vessels.

Description of Charcoal: Both dried and fresh charred tissues are similar. Generally the outermost tissues are lost though most of the cortical tissues may survive. The ground tissue of both the cortex and the pith becomes

highly vesicular (Figs. 6 to 7, Plate 50 and Figs. 3 to 4, Plate 51). Cell walls are not definable within this tissue. The vascular bundles throughout this tissue are preserved well, (Fig. 9, Plate 50) though both the xylem parenchyma and the phloem are reduced to solid carbon, (Fig. 10, Plate 50). The fibre sheath is easily identifiable though somewhat distorted (Fig. 1, Plate 51). The charcoal is black throughout shiny to glassy and rather brittle.

CURCUMA DOMESTICA

ZINGIBERACEAE

Morphology: Morphologically this is similar to Alpinia galanga though narrower at only 1 to 1.5 cm across. The rhizome is circular in transverse section and internodes are 1 to 4 cm long. The rhizome branches regularly.

Anatomy: Internal to a narrow epidermis is a region of parenchyma between one and 6 cells thick. Internal to this are 6 layers of tangentially flattened rows of cork cells. The cortex and pith are separated by an indistinct endodermal layer. Vascular bundles occur in both the cortex and the pith.

Epidermis and Cork Layer: The epidermis consists of a single layer of rectangular unthickened cells approximately 10 μ m across. Internal to this is a region of parenchyma made up of between 1 and 6 layers of either

irregular radially or tangentially elongated cells. Internal to this are 3 to 6 layers of cork cells and internal to this the cortex.

Ground Tissue: This is similar throughout the cortex and the pith and is made up of cells polygonal to circular in transverse section 70 to 100 μm across. These are longitudinally elongated. Idioblastic oil cells occur throughout the tissue. These are similar in both size and shape to other cells of the ground tissue.

Endodermis: This is an indistinct layer of rectangular cells 20 to 25 μm across.

Vascular Tissue: Vascular bundles occur in both the pith and the cortex and are similar in terms of both size and concentration. These are circular to ovoid in shape consisting of phloem and xylem in very irregular arrangements. Many vascular bundles occur directly adjacent to the internal endodermal wall. Groups of vessels in circular or linear arrangements. Vessels are polygonal in transverse section, thin walled and around 45 μm across. Phloem occurs either adjacent to or surrounding the xylem.

Description of Charcoal: Tissue charred from the fresh state is significantly different from tissue charred from the dried state. Preservation of tissue dried prior to charring is good. The outermost tissue to survive is the

cork layer (Figs. 6 and 7, Plate 51). The ground tissue of the cortex and pith internal to the cork also survives intact, although tension fracture cavities may occur especially between the cork and the cortex (Figs. 6, 8 and 9, Plate 51 and Figs. 2 to 3, Plate 52). Vascular tissue, due to the reduction of the phloem to solid carbon is harder to identify as such, in transverse section (Fig. 10, Plate 51 and Fig. 1, Plate 52). However in longitudinal section cavities caused by the breakdown of this tissue and adjacent parenchyma are easily visible (Fig. 4, Plate 52). Tissue charred from the fresh state becomes highly compressed against the internal wall of the outer cortex, leaving large cavities along the length of the tuber (Figs. 5 to 6, Plate 52). The charcoal is black throughout dull and rather soft.

ZINGIBER OFFICINALE

ZINGIBERACEAE

Morphology: The rhizome, similar to both Alpinia galanga and Curcuma domestica is regularly branching, rather stout and with short internodes. It is slightly dorsoventrally flattened and narrowed at each mid internode region. The rhizome is 2 to 4 cm across.

Anatomy: The arrangement of tissues is similar to that of Curcuma domestica having a narrow epidermis internal to which lies a thin layer of parenchyma and a cork layer.

The ground tissue of the cortex and the pith is similar throughout being spherical 50 to 60 μm across with well developed air spaces. The endodermis is a single layer of rectangular cells with a prominent casparian strip. Vascular tissue is limited to bundles placed close to the internal wall of the endodermis, with the exception of a few bundles in the cortex. The vascular bundles are irregular in shape 100 to 150 μm across and are amphicribal concentric in arrangement. Vessels are polygonal in transverse section approximately 30 μm across.

Description of Charcoal: Differences occur between tissues charred from the fresh state and tissues charred from the dried state. Tissues dried prior to charring become highly vesicular (Figs. 7 to 10, Plate 52). Much of the tissue is reduced to solid carbon or compressed by the formation of small vesicles. Vascular tissue is extremely hard to identify within this deteriorated tissue (Fig. 2, Plate 53). Tissue charred from the fresh state is less vesicular but contains larger cavities within it (Figs. 4 to 5, Plate 53). The tissue between the cavities is better preserved and actual cell walls are easily identifiable. The internal walls of the vessels have the impressions of parenchyma cells upon them (Figs. 7 to 8, Plate 53). The charcoal resulting from dried charred

tissue is hard and glassy whereas the charcoal resulting from fresh charred tissue is dull and very much softer. Both are black throughout.

ACORUS CALAMUS

ARACEAE

Morphology: Shoots arising from a long branched rhizome circular in transverse section 1 to 1.5 cm across. It gives rise to fibrous shoots from all surfaces.

Anatomy: Internal to an epidermis is a narrow outer parenchymatous cortex internal to which is a much wider aerenchymatous region. An endodermal structure separates the cortex from an aerenchymatous pith. Vascular tissue is concentrated in a narrow region internal to the endodermis but also occurs in the central pith and cortex.

Epidermis: Single layer of unthickened rectangular cells 15 μm across.

Cortex: Immediately internal to the epidermis are 3 to 4 layers of cells circular to tangentially elongated in transverse section 30 to 40 μm across. Internal to this is an aerenchymatous ground tissue made up of cells circular in transverse section and circular to barrel shaped in longitudinal section. The cells are 30 to 40 μm across. The cells may be in rows or plates forming intercellular air spaces 100 μm across and up to 260 μm long. The aerenchymatous ground tissue of the cortex is

similar to that of the pith.

Endodermis: A single layer of rectangular cells approximately 10 μm across. There is a prominent casparian stip. An endodermis separates the cortex and the pith but also surrounds any vascular tissue in the cortex.

Vascular Tissue: Most of the vascular tissue is concentrated within the tissues immediately internal to the endodermis. Vascular bundles are circular in transverse section 75 to 250 μm across. They are amphivasal concentric in arrangement with a complete or near complete ring of xylem. Trachery elements are circular to irregular in shape 30 μm across. The bundles are surrounded by a parenchymatous sheath and in the cortex by an endodermal layer.

Description of Charcoal: Both dried and fresh charred tissues are similar. The epidermis and outer parenchymatous cortex are reduced to a solid layer of carbon. Internal to this the aerenchymatous ground tissue of the cortex and pith are well preserved. The cells are compressed and become narrow solid plates around the intercellular air spaces (Fig. 9, Plate 53 and Figs. 1, 3 and 4, Plate 54). Vascular tissue is preserved well with the exception of the phloem which is reduced to solid carbon as is the endodermis (Fig. 10, Plate 53 and Figs 1

to 2, Plate 54). The charcoal is black to pale brown in colour dull to glassy in texture, hard and brittle.

ARUM MACULATUM

ARACEAE

Morphology: Shoots appear from a persistent swollen tuber at the base of the stem. This lies either vertically or obliquely below the ground. A new tuber is produced each year, previous years tubers lie in succession below the present years in progressive states of decay. Tubers are ovoid, multinodal, and covered in roots. Large tubers may reach 3 cm across and 5 cm long though most are a little smaller.

Anatomy: Internal to an epidermis is a thin parenchymatous region internal to this a narrow cork layer. Ground tissue internal to this contains a network of vascular bundles. Winton and Winton (1935) examined this species.

Epidermis and Cork Layer: The epidermis is a single unthickened layer of cells internal to which are 1 to 3 layers of irregular parenchyma cells. Internal to this are 4 to 5 layers of tangentially flattened cork cells in rows.

Ground Tissue: Composed of irregularly rounded, more or less isodiametric cells with few intercellular air spaces. The cells are approximately 50 μm across and vary little throughout the tuber.

Vascular Tissue: Vascular bundles are widely separated and run apparently randomly throughout the ground tissue. They are circular in transverse section and amphivasal concentric in arrangement 100 to 150 μm across. The xylem ring is rarely complete and is made up of elements, polygonal in transverse section with circular lumina 10 μm across.

Description of Charcoal: Tissue charred from the fresh state was not preserved well enough to survive normal taphonomic processes. The internal tissues become highly compressed against the internal epidermal wall leaving a shell like charred remain. This was, due to its large size, easily broken and would not normally survive. Tissue dried prior to charring does survive but varies greatly in the form of charcoal even within the tissue of the same tuber. Commonly the outermost tissues become more or less solid charcoal (Fig. 6, Plate 54). Cells of the ground tissue may be preserved so that each has discernable cell walls but a solid cell contents (Figs. 7 and 8, Plate 54). The ground tissue becomes highly vesicular with no discernable cell walls (Figs. 9 to 10, Plate 54 and Fig. 1, Plate 55). Larger vesicles within the tissue may have very clear impressions of individual cells on their internal walls (Figs. 2 to 3, Plate 55). Other cells may be preserved with narrow friable cell

walls and no cell contents (Fig. 4, Plate 55) or with discernable starch grains (Fig. 6, Plate 55). No remains of vascular tissue were visible. The charcoal is black to light brown in colour ranging from being dull to glassy in texture, but always rather hard.

CROCUS SATIVUS

IRIDACEAE

Morphology: The perennating organ of this species is a tunicate corm, more or less spherical with an apical meristem lying in a slight depression directly opposite a base that gives rise to fibrous roots. The corms measured 2 to 2.5 cm across.

Anatomy: Internal to an epidermis is a cork layer. This is missing in certain regions creating a rather uneven surface. Internal to this is a parenchymatous ground tissue through which runs a system of vascular bundles.

Epidermis: The epidermis is made up of a single layer of thickened rectangular cells. At intervals regions of cork cambium form internal to this. In these cases the outer tangential wall of the epidermis tends to be thickened.

Ground Tissue: This is made up of isodiametrically polygonal cells 30 to 40 μm across with few intercellular air spaces. The ground tissue is similar throughout.

Vascular Tissue: Vascular bundles are widely spaced and run apparently randomly throughout the ground tissue.

These are irregular to circular in shape 50 to 250 μm across. Small bundles contain only phloem and parenchyma. Larger bundles are amphicribal concentric in arrangement having a core of vessels embedded within a sheath of phloem.

Description of Charcoal: All remains of roots, tunic and apical shoots are removed on charring. The apical meristem is marked by small circular scars at the base of the apical depression. In tissue dried prior to charring the external tissues are reduced to solid carbon internal to which the ground tissue is preserved well (Figs. 7 to 9, Plate 55). The parenchyma becomes a little vesicular but is easily recognisable as such. Vascular tissue is not preserved well, the phloem either being reduced to solid carbon (Fig. 10, Plate 55) or breaks down to form a cavity (Figs. 1 and 2, Plate 56). The xylem is discernable in both. Tissue charred from the fresh state suffers damage caused by tension fractures leaving cavities throughout the tissue (Figs. 4 to 6, Plate 56). Otherwise preservation is similar to that of the tissue dried prior to charring. The charcoal is black throughout, dull in texture and very hard.

Morphology: Along the narrow roots of this species are swollen regions often forming large parts of the root. These are often terminal and may measure up to 15 cm long and 3 cm across. The tubers are transversely ridged.

Anatomy: Internal to a narrow epidermis is a region of thickened cells internal to which is a cork layer. Internal to this are parenchymatous cortex and pith separated by an epidermis and pericycle.

Epidermis and Cork Layer: A single layer of epidermal cells is made up of cubic cells 30 μm across. This is often ruptured. Internal to this is a region of thickened cells polygonal in shape and slightly longitudinally elongated 30 to 35 μm across. Internal to this lie 8 to 9 layers of cork cambial cells in rows.

Ground Tissue: The ground tissue of the cortex and pith is similar made up of cells circular in transverse section and polygonal in longitudinal section either isodiametric or slightly elongated. Cells measure 50 to 100 μm across. Intercellular air spaces are common.

Endodermis and Pericycle: The endodermis is made up of a single layer of rounded rectangular cells 25 μm across with a prominent casparian strip. The pericycle, internal to the endodermis is made up of a single layer of cells to the endodermis but elongated in longitudinal section.

Vascular Tissue: Immediately internal to the endodermis and pericycle lie alternate regions of phloem and xylem adjacent to each other. The phloem consists of small bundles 50 μm across. The xylem is arranged in linear groups radially oriented. Vessels are thin walled, polygonal in transverse section with circular lumina. They become larger away from the pericycle ranging in size from 6.7 μm across to 70 μm across. Large vessels may be isolated from the linear arrangement and will then be surrounded by parenchymatous sheath which is again surrounded by a fibre sheath. Each is one cell thick. A similar pattern of parenchyma and fibres surrounds the linear arrangements of vessels.

Description of Charcoal: Charcoal derived from fresh tissue differs significantly from charcoal derived from dried tissue. If dried prior to charring tissue is preserved in a state so that most of the cell layers described external to are easily identifiable. However the outermost layers to survive are within the cortex rather than the cork layers or the epidermis (Fig. 7, Plate 56), with the exception of a few isolated cases (Fig. 10, Plate 56). The ground tissue (Figs. 1 to 2, Plate 57), and xylem (Fig. 9, Plate 56) survive intact though the endodermis, pericycle and phloem are all reduced to solid carbon, (Fig. 9, Plate 56). Charcoal

derived from fresh tissue is not preserved as intact as charcoal derived from dried tissue. The tissue is highly compressed by vesicles radiating out from a central mass of solid and vesicular carbon (Figs. 3 to 7, Plate 57). The central tract of carbon has definable cell walls though these are very much distorted. Raphides do survive in some of the cells (Fig. 8, Plate 57). No vascular tissue survives nor is the endodermis or pericycle definable. The charcoal derived from dried tissue is black throughout and very soft. The charcoal derived from fresh tissue is also black throughout but is hard and glassy in texture.

POLYGONATUM X HYBRIDUM

LILIACEAE

Morphology: Shoots arise from a stout truncated rhizome. This branches regularly and is 2 to 3 cm across. Nodes are also 2 to 3 cm apart. The mid-internodal region may be slightly narrowed. Shoots arise from a depression on the dorsal surface of the terminal internode on a rhizome or rhizome branch. Ervin and Ervert (1970) have examined P. canaliculatum.

Anatomy: Internal to an epidermis is a more or less uniform ground tissue through which runs a somewhat apparently random and truncated vascular system.

Epidermis: A single layer of rectangular cells 30 μm

across. These are unthickened and have a thick cuticle.

Ground Tissue: Immediately internal to the epidermis is a region of tangentially elongated cells 70 to 80 μm across. This layer is 7 to 8 cells across. Internal to this the cells become circular in transverse section 80 to 100 μm across and elongated longitudinally up to 150 μm . In the outer tissues much larger cells were observed within the tissue. These were circular to ovoid in transverse section up to 100 μm across and longitudinally elongated up to 450 μm . Their function was undetermined.

Vascular Tissue: Vascular bundles run apparently randomly through the ground tissue as well as forming a rather incomplete ring internal to the tangentially elongated cells of the outer tissue internal to the epidermis. Bundles are amphivasal concentric in arrangement although this may be a little distorted in larger bundles. Vessels are polygonal in transverse section and connected in chains but rarely form a complete ring. Vessels are 30 to 35 μm across.

Description of Charcoal: Both dried and fresh charred tissues were similar. Morphologically the rhizome is preserved well with nodes (Fig. 10, Plate 57), and shoot scars (Fig. 1, Plate 58) being easily identifiable. The internal tissues are however deteriorated to some considerable extent. The outermost tissues become solid

carbon (Fig. 2, Plate 58) and many of the other tissues become partially solid or vesicular separated by large vesicles, (Figs. 3, 4 and 6, Plate 58). Large vesicles have parenchyma cell impressions upon them, (Fig. 9, Plate 57 and Fig. 7, Plate 58). Vascular tissue is identifiable (Fig. 5, Plate 58) although the phloem commonly breaks down to leave a cavity. The charcoal is black throughout dull to glassy in texture hard and rather brittle.

TAMUS COMMUNIS

DIOSCOREACEAE

Morphology: The perenating organ of this species is a massively tuberous structure derived from the swelling of the first epicotyledonary internode (Ayensu 1972). The tuber is vertically elongated up to 45 cm and up to 15 cm across. It often branches downwards though is usually somewhat contorted. Shoots arise from the flattened apical surface and fibrous roots arise occasionally from the surface.

Anatomy: Internal to a thick periderm is a very narrow cortex internal to which is a continuous cambium. Internal to this is a massive parenchymatous pith through which runs a system of vascular bundles. Both Sablon (1902) and Ayensu (1972) have examined this species.

Periderm: Internal to an outer distorted layer of very irregular and highly thickened cells are 4 to 5 layers of

cork cells, tangentially flattened and in rows. The periderm is approximately 150 μm across.

Cortex: Circular to tangentially elongated in transverse section cells 50 μm across. This layer is approximately 20 cells across some of the cells containing raphides. Internal to this layer is a continuous region of cambial cells. These are in rows and tangentially flattened. The layer is 4 to 5 cells across.

Pith: Made up of rectangular cells with their long axis radially oriented though tissue at the centre of the pith is more irregular. The cells are approximately 50 by 120 μm across. Throughout this tissue are idioblastic cells. These are 250 μm long, 100 μm wide and circular in longitudinal section. These contain large raphide bundles over 200 μm long.

Vascular Tissue: Vascular bundles occur apparently randomly throughout the pith. These are more or less ovoid in transverse section and collateral in arrangement made up of circular bundles of tracheids internal to a smaller irregular mass of phloem. Tracheids are rounded in transverse section and often rather interwoven. They are 30 to 40 μm across. Bundles are commonly 225 by 100 μm .

Description of Charcoal: Both dried and fresh charred tissues were similar. The inner and outer tissues of the

cortex and pith were not easily distinguishable from each other. The ground tissue throughout the tuber is deteriorated to a very characteristic vesicular carbon (Figs. 8 to 10, Plate 58). The vascular tissue is, with the exception of the phloem, preserved well (Figs. 1 to 2, Plate 59). The phloem or even a deteriorated product is not easily identifiable. The large raphide bundles within the pith are easily identifiable and extremely characteristic (Figs. 3 to 4, Plate 59). The charcoal is brown to black in colour dull in texture and reasonably hard.

ORCHIS MASCULA

ORCHIDACEAE

Morphology: Each plant has two tubers, one of the present year and one of the previous year. The latter is somewhat shrivelled. The tubers are derived from swelling of the root tissue. They are ovoid though rather flattened vertically being approximately 2 to 4 cm across in transverse section, and up to 5 to 6 cm long.

Anatomy: Internal to a thickened and irregular periderm is a uniform ground tissue with a polystelic vascular system. Sharman (1932) examined the anatomy, morphology and life history of this species.

Periderm: This is highly thickened and rather irregular in width ranging from 50 to 150 μ m across.

Ground Tissue: Immediately internal to the periderm is a narrow region of cells radially elongated up to 100 μm . Internal to this the cells enlarge to become irregular in shape and up to 400 μm across.

Vascular Tissue: A network of steles runs throughout the ground tissue. These are circular in transverse section 200 to 400 μm across and having an endodermis with a prominent casparian strip. Internal to the pericycle is an indistinct pericycle and a core of phloem. Embedded within this are trachery elements, thin walled and polygonal in transverse section 20 to 25 μm across.

Description of Charcoal: Tissue charred from the fresh state and tissue charred from the dried state were similar. The tissues deteriorate considerably so that the outer ground tissue and the periderm are not easily distinguishable from each other. The central ground tissue becomes solid and somewhat vesicular although cell walls are still discernable (Figs. 5 to 7, Plate 59). Vascular tissue deteriorates considerably so that only the remnants of the xylem are discernable (Fig. 10, Plate 59). The charcoal is black throughout, glassy and rather hard.

CHAPTER SEVEN - RESULTS III - ARCHAEOLOGICAL CHARCOAL

7.1 INTRODUCTION

Presented here are three examples of archaeologically preserved vegetative parenchymatous tissue. Although a number of other samples of archaeological material have been examined, it was decided to limit the samples described to these three. These vary considerably and therefore adequately illustrate the relevant points brought out by the modern material, both dried and fresh. Since this research project has attempted to examine the overall potential for identification of preserved plant tissues and has not attempted to examine any particular archaeological question, the inclusion of many similar archaeological remains from different archaeological sites, though interesting, has no direct bearing on the present research.

The three examples illustrated here vary considerably in their state of preservation as well as their anatomy and original morphology. For this reason the level to which identification has been possible also differs. The three archaeological remains are rhizomatous remains from Aqaba, (McQuitty and Hather forthcoming) root tuber remains from Stonehenge (Richards forthcoming), and stem tuber remains

from Wadi Kubbaniya in Egypt (Hillman, Madyeska and Hather 1988).

7.2 AQABA REMAINS

The excavation of the early Islamic town of Aqaba in southern Jordan revealed a cooking area containing ten 'tabun' type ovens (McQuitty 1984). Associated with these were both ash and charred plant fragments. The larger fragments, over 300 um across, were separated from the matrix by sieving. These were then washed in acetone. The charred remains contained only a few seeds, the majority of the remains consisting of approximately sixty per cent wood and 40 per cent parenchymatous tissue.

The fragments of parenchymatous tissue fell into two classes: firstly small, irregular, but generally isodiametric fragments less than 3 mm across and secondly larger fragments up to 3.5 cm long and elongated along one axis. Vascular tracts visible under low magnification, running along the axis of the larger fragments suggested that these were the remains of a rhizome rather than any other type of organ. The type of preservation as well as the morphology indicated that these could not be the remains of non-vegetative parenchyma.

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The fragments of parenchymatous tissue fell into two classes: firstly small, irregular, but generally isodiametric fragments less than 3 mm across and secondly larger fragments up to 3.5 cm long and elongated along one axis. Vascular tracts visible under low magnification, running along the axis of the larger fragments suggested that these were the remains of a rhizome rather than any other type of organ. The type of preservation as well as the morphology indicated that these could not be the remains of non-vegetative parenchyma.

Fresh transverse and longitudinal fracture planes of the larger fragments and irregular fracture surfaces of the smaller fragments were observed under scanning electron microscopy. A ground tissue of parenchyma contained a number of randomly placed vascular and fibre bundles, (Figs. 1 and 2, Plate 65). The vascular bundles were all oriented in the same direction and no epidermal, peridermal or endodermal structures were found. This indicated, together with the general curvature of the larger fragments that these remains were fragments of a much larger organ. The ground tissue was composed of more or less isodiametric cells, although those close to either fibre or vascular bundles were elongated in an axis radiating out from the centre of the bundles in transverse section (Figs. 3 and 4, Plate 66).

Fibre bundles, between 40 and 60 μm across, consisted of fibres with lumina between 5 and 15 μm across, smaller fibres being at the periphery of the bundle. These are illustrated by Figures 1, 2 and 10 on Plate 66.

The vascular bundles were all surrounded by a fibre sheath, which varied in thickness depending on the position of the bundle. Assuming that the phloem of the vascular bundles lay external to the xylem the outer bundles of the tissue were capped with fewer fibres (Fig.

4 and 5, Plate 65) compared with bundles in tissue further towards the centre of the rhizome (Figs. 6 to 8, Plate 65). In both cases the fibre sheath was wider at the xylem pole than at the phloem pole. At the latter the sheath was 4 to 5 cells thick in most bundles. The sheath varied between 10 cells thick in outer bundles and up to 25 cells thick in inner bundles at the xylem pole.

The xylem is composed of several large vessels between 50 and 80 μm across. These are associated with smaller vessels and parenchyma, (Figs. 9 and 10, Plate 65). The tissue of the phloem has not survived, as is the case with all but very few of the charred tissues of this type. The breakdown of the phloem has left a cavity visible in the vascular bundles as illustrated in transverse section in Figures 4 and 5 (Plate 65). The tissue is arranged in a collateral organization, bundles measuring 200 to 350 μm by 300 to 550 μm across.

Observations of smaller fragments of charred parenchymatous tissue revealed a similar composition to the larger fragments described above.

Certain characters, such as some of those described above are diagnostic for certain hierarchical taxonomic levels. The characters of the tissue in the particular combination

described above lead to certain conclusions. The relative positions of the vascular bundles and their structure indicate that these are the rhizomatous remains of a monocotyledon. It has already been established that these are probably rhizomatous remains and certainly represent small fragments of a much larger organ, possibly up to 5 or 6 cm across. The specific character states such as the positions of the vascular and sclerenchymatic tissues, narrow the possible identification down to only a few genera. Assuming the Early Islamic flora is basically similar to that of the present day, the list of possible taxa these remains could represent is narrowed further. A combination of the character states and additional information concerning the local flora leads to an identification of these remains as those of the genus Sparganium. It has not been possible to identify these remains further to the level of species.

The state of preservation of these remains is good. Tissues such as the xylem parenchyma have survived intact even though the tissue of the phloem has deteriorated. The ground tissue has been preserved intact without the formation of vesicles or tension fractures. It has been indicated in Chapter five, above, that such preservation would indicate that the tissues contained a minimum water content on charring. Had the tissues been fresh rather

than dried on charring then the presence of vesicles and tension fractures, deteriorated xylem parenchyma and generally poor preservation would be expected.

The ethnographic literature indicates that the rhizomes of Sparganium species may be cooked and eaten as an emergency food in times of famine (Uphof 1965). While it is possible that Sparganium may have formed part of the diet of the inhabitants of early Islamic Aqaba it is more likely that since these remains were dried prior to charring that they represent fuel for the oven fire rather than food.

7.3 STONEHENGE REMAINS

These remains were of whole and fragmented organs, ovoid in shape and pointed at both ends. In size they ranged from between 5 to 9 mm across and 1 to 1.5 cm long. Even under high magnification the external surface bore no features of interest. One of the two pointed ends bears the scar of a point of attachment. In all cases this had deteriorated beyond a state at which diagnostic features may be recognised.

Both the surfaces of fragments and the fractured internal surfaces of whole organs were observed under scanning

electron microscopy. Two types of preservation were observed.

A: The better of the two types of preservation were characterised by the largest of the remains, a fragment of an ovoid organ, that if whole would have measured 1.5 cm long and 9 mm across. A fracture plane along the longitudinal axis showed a highly vesicular ground tissue containing large cavities (Figs. 1 to 5, Plate 67). The cavities were ovoid, the internal walls of which displayed the compressed cell walls of the constituent parenchyma. All the cavities ran along the same parallel, transverse planes, and were all between 500 μ m and 1 mm across. The ground tissue was highly vesicular and individual cells indeterminate from small vesicles. Running down the central long axis of the organ is an obvious central vascular tract (Fig. 1 and 4, Plate 67). Xylem elements were discernable but highly deteriorated.

A transverse fracture plane through another fragment showed a pattern of vesicles typical of an elongated organ with a central vascular tract and radiating parenchyma (Figs. 6 to 9, Plate 67). The pattern of vesicles visible in a longitudinal fracture plane was indicated by surfaces in the transverse surface of compressed parenchyma. The external surface of the organ was shown to be composed of

a thickened epidermal or peridermal region (Fig. 10, Plate 67).

The ovoid shape and detachment scar indicate that the organ is a swollen region of a narrower stem or root. The single detachment scar indicates that this was terminal. The central vascular tract suggests that the organ is likely to be of root rather than stem tissue origin. Since also the organ lacked any external scars of nodes or scale leaves, this indicates that this organ is of root origin. Visible on Figures 6 to 8 on Plate 67 is an agglomeration of a thicker carbon mass containing small cavities close to the outer tissue of the organ. It is possible that this is of vascular origin though other characteristics displayed by the organ suggest that these are the remains of root tubers. If the feature is not of vascular origin then the remains may be likened to small root tubers similar to that of Lathyrus linifolius. However since these tissues are considerably deteriorated it is very difficult to assign these remains to any specific taxon.

B: The second of the two types of preservation is represented by fragments of smaller organs no more than 1 cm long and 5 mm across. Preservation is poor the tissues of the organs being compressed to a very high degree

against the internal walls of the organ leaving large vesicles in their place, (Figs. 1 to 10, Plate 68). The compressed tissue is represented by almost solid carbon containing small vesicles. No cellular remains are visible in a fracture plane through this. The internal walls of the vesicles do show signs of compressed parenchyma typical of such preservation, (Figs. 6, 9 and 10, Plate 68).

Although no anatomical characters could indicate whether these remains are of stem or root origin, the morphology, similar to the remains described previously, indicate that these are the remains of small ovoid tubers. By association they may be considered to be similar in other respects to the previously described class of remains although differing in the state of preservation.

The poor state of preservation of both classes of remains suggest certain charring conditions. The high degree of the deterioration of the tissues and the strong pattern of vesicle formation indicates that the tissues were fresh (wet) on charring, the second of the described remains possibly having a higher water content than the first.

7.4 WADI KUBBANIYA REMAINS

The charred parenchymatous tissues recovered from Wadi Kubbaniya illustrate how, despite great age, good preservation of a large number of anatomical and morphological characters may lead to the identification to the level of species. The remains date from the Late Palaeolithic in Upper Egypt and therefore offered a unique opportunity to examine the role of parenchymatous foods in pre-agrarian diet.

Described here are the remains of whole and fragmented tubers; these form only a fraction of the plant remains recovered. These are described here in terms of their identification and preservation. For a more detailed discussion of the palaeo-economic and ethnobotanical significance of all the remains recovered from the site readers are referred to Hillman, Madeyska and Hather (1988).

The whole and fragmented organs are between 5 mm and 1.5 cm long and are associated with small fragments of charred parenchymatous tissue, irregular in shape between 1 and 5 mm across. Two types of characters were observed, those associated with rhizome detachment scars and those derived from fracture planes through the tissue of the tubers.

Some fragments displayed both types of characters, others only the latter.

A: Small scars visible on the external surfaces of the fragmented and whole organs suggested that these organs were swollen regions of a much narrower root or stem system. These detachment scars were well preserved and characters of diagnostic value were present. These are illustrated by Figures 1 to 8 on Plate 69.

The detachment scars were circular in transverse section as they appeared on the surface of the tuber. Due to erosion of the tuber surface and the resistance to erosion of the scar itself, many of the scars protruded slightly from the surface of the tuber. The scars ranged from between 500 μ m and 1 mm across in diameter. The most noticeable character of the scars is the large amount of structural tissue. This is made up of fibres of the sclerenchyma, lignified and resistant to deterioration on charring. A peridermal layer between 2 and 3 cells deep surrounds the circumference of the scar, (Fig. 3, Plate 69). Below this the scar is made up of many vascular bundles each surrounded by a thick fibre sheath, between 2 and 6 cells deep. Organization of the vascular tissue in this manner suggests that the remains are derived from stem rather than root tissue. The remains are therefore

of stem tubers and the scars left by the detachment of narrower rhizomes.

Figure 4 on Plate 69 shows a single vascular bundle, its outermost tissues to the left of the Figure. The phloem and any parenchyma has deteriorated but two metaxylem vessels have survived. The whole bundle is surrounded by a parenchymatous sheath although this has become on charring a solid ring of carbon. Comparing this with the vascular bundles from the rhizome detachment scar from another specimen (Fig. 8, Plate 69), here the outer tissues are to the bottom of the Figure. The vascular tissues have deteriorated completely although the fibre sheath has survived and the lumina of the individual cells are easily visible. Where the detachment scars contain a central fissure (Figs. 5 and 6, Plate 69), this would represent the deterioration of a central parenchymatous pith. Where no such fissure exists (Figs. 1 and 2, Plate 69), the vascular tissue extends to the centre of the scar.

Scars of this type occurred at either of the two ends of the ovoid tuber as well at other points on the tuber surface. Up to 3 scars occurred on any one tuber or tuber fragment.

B: Fragments of tubers with fracture planes showing the internal anatomy in longitudinal and transverse section as well as oblique fracture planes were observed. The tubers were seen to be made up of a parenchymatous ground tissue through which ran a more or less randomly placed vascular system.

The parenchymatous ground tissue was composed of more or less isodiametric cells 20 to 25 μm across. The walls were seen to be unthickened as a result of charring. No middle lamella were seen and no cell contents were observed. The ground tissue is visible in all the fragments illustrated by Figures 9 and 10 on Plate 69 and Figures 1 to 10 on Plate 70. It is however best illustrated on Figure 4 on Plate 70.

The tissue of the vascular bundles is organized in an amphivasal concentric arrangement and were circular in transverse section between 50 and 100 μm across. In all cases the tissue of the phloem has deteriorated leaving a hollow channel at the centre of the vascular bundle. In some cases the whole of the vascular tissue has deteriorated leaving a larger hollow channel (Figs. 5 to 10, Plate 70).

The fragments of parenchymatous tissue and whole and fragmented tuber remains all contained similar anatomical features.

It has been established that these remains are of stem tuber. The arrangement of vascular tissues in the rhizome detachment scar as well as the apparently random nature of the vascular system in the tuber itself suggest that these are monocotyledonous. Although the ground tissue is typical of the Cyperaceae it is also the type found in other families such as the Gramineae and the Sparganiaceae. An examination of the modern flora extrapolated to take into account the differences between the present and Late Palaeolithic physical conditions of the area narrows the possible taxa represented by these remains down to a few species: Cyperus rotundus, Cyperus esculentus and Scirpus maritimus/tuberosus.

The Scirpus maritimus/tuberosus aggregate of taxa have stem tubers although these appear as more caudex type rootstock organs rather than tubers in the strict sense. These also tend to be larger and more rounded. This reduces the possible taxa to two species of Cyperus, C. rotundus and C. esculentus. These two species may be distinguished by the relative positions of the tubers in the rhizome system of the plant. C. esculentus has tubers

that are terminal on the rhizome system, the apical bud at the distal end of the tuber being dormant. C. rotundus has tubers that are either terminal or along the length of the rhizome system.

The tuber remains that have been described here have in a number of cases more than one detachment scar left by a rhizome. This suggests that these fragments are the remains of tubers that formed along the length of a rhizome system. That is to say that these are the remains of C. rotundus rather than C. esculentus. The other remains associated with these that may not be distinguished by the presence of rhizome detachment scars may be, on this account, either of the two species.

In general it may be said that C. rotundus and C. esculentus are similar anatomically with the exception of the above character. However an examination of a wide variety of C. rotundus tubers indicates that these may vary considerably in the amount of structural tissue in the rhizome. The vascular sheath varies in width from one cell thick to seven cells thick. Vascular bundles also vary in having a complete ring of xylem elements around the phloem in the amphivasal arrangement of the concentric vascular bundles. To having a ring composed of only a few vessels with a number of gaps. Plants growing in drier

conditions have more xylem and structural tissue than those growing in waterlogged conditions. These also have a more heterogenous rhizome - tuber system than those growing in waterlogged conditions.

C. esculentus varies far less in these respects having little structural tissue in the rhizome and usually incomplete rings of xylem in the amphivasal concentric vascular bundles of the tubers. It also has a stable heterogenous rhizome - tuber system. Since the fragmented remains described here generally contain vascular bundles with complete rings of xylem in the vascular bundles of the tubers these may be said to be the remains of C. rotundus tubers rather than those of C. esculentus.

CHAPTER EIGHT - DISCUSSION

8.1 INTRODUCTION

The broad aim of carrying out this research was to attempt to recognise characters with which to identify the charred archaeological remains of vegetative parenchymatous storage organs. This has been achieved by the careful examination of the effects of charring upon a wide taxonomic, morphological and anatomical range of taxa. The primary aim was to define useful diagnostic characters on a general basis, and the second aim of this research was to examine as many different taxa as time would allow, in order to build up a body of reference information. With these in mind, it was decided to concentrate on the selection of a limited number of taxa that would adequately represent the very varied classes of organs and tissues that constitute vegetative storage organs.

In this discussion methods of identification of charred vegetative parenchymatous storage organs will be considered. Before this however, relevant anatomical and morphological aspects of the research will be considered. Following this pre- to post- preservation aspects of taphonomy affecting the survival and identification of vegetative storage organs will be examined. Methods of

identification will then be discussed and presented. Following this the applications of the research will be examined and finally to sum up a list of conclusions will be presented.

8.2 CLASSIFICATION OF MORPHOLOGY

In carrying out this research it has been necessary to reassess the terminology with which the types of organs under examination could be described. Definitions of morphological types already existing largely failed to encompass the wide range of variation in morphology presented by the taxa under examination here. For this reason a more extensive classification of morphological types of vegetative storage organs has been developed and used throughout this thesis.

An appreciation of the terms outlined in this classification is necessary if a full understanding of the descriptions of charred vegetative storage organs and methods for their identification is to be reached. Terms such as rootstock, rhizome and stolon are surrounded by a certain amount of confusion and ambiguity. An understanding of the way in which such terms are used here is important if the methods of identification presented are to be used successfully.

It is hoped that in describing archaeological remains of vegetative storage tissues a standardized morphological terminology will be used. This will not only prevent a great deal of confusion but also allow compatibility between descriptions leading to a greater number of identifications.

8.3 PRE-PRESERVATION, PRESERVATION AND POST-PRESERVATION CONDITIONS AFFECTING SURVIVAL AND IDENTIFICATION

The results presented in Chapters five and six show that many taxa may, on charring, form one of several different classes of charcoal depending on the state of the tissue prior to charring. Size of fragment and water content on charring both have a profound effect on the results of charring. It is possible therefore, that some inference may be drawn, concerning the state of the tissue at the time of preservation from the appearance of the charred tissue.

Tissues often show variation in the degree of the effects of charring through the formation of vesicular or tension fracture cavities or the reduction of the ground tissue to solid, vesicular or otherwise deteriorated charcoal. If the effects of charring vary, it is always the case that

the less the degree of deterioration, the drier the tissues are on charring. In tissues of archaeologically preserved taxa where such variation is known to occur, states of particularly good preservation or particularly poor preservation can confidently be said to be representative of respectively dried or fresh (wet) tissues at the time of charring.

The ability to distinguish between dried and fresh charred tissues is demonstrated by the experimentally charred tissues of the roots of Daucus carota (Plates 22 to 24) and Asphodelus aestivus (Plates 18 and 19) and Ranunculus ficaria (Plates 6 and 7), amongst many others. This phenomenon can also be demonstrated by using two of the archaeological remains examined in this research, described in Chapter 7.

The rhizomatous remains recovered from oven sites in Aqaba in southern Jordan, (Plates 65 and 66), are particularly well preserved and lack any signs of deterioration, with the exception of the phloem tissues. Even the extremely fragile tissues of the xylem parenchyma are preserved in good condition. This would indicate that the tissues were dried prior to charring, possibly to facilitate their use as tinder for the oven fires.

In contrast the root tuber remains recovered at the Stonehenge environs site (Plates 67 and 68) show a particularly poor state of preservation. Displaying similar results to the experimentally charred fresh root tuber of Lathyrus linifolius (Plates 18 and 19), these remains were most probably fresh (wet) on preservation by charring.

The size of the charred organ also has an effect on the state of preservation. Large organs are more likely to be damaged by the formation of vesicles on charring than are smaller organs. This is demonstrated by the experimentally charred tissues of the tuber of Bryonia dioica (Plates 12 to 13) and the root of Brassica campestris (Plate 14). Both are large organs compared with poor preservation compared with the better preservation displayed by numerous smaller organs.

Several factors may cause organs or tissues of certain taxa to deteriorate not only to an extent that creates difficulty in identification but also to a degree that prejudices the charcoal's survival in the post-preservation environment, that is, both survival from preservation to a point directly prior to excavation as well as during the processes of recovery and sorting.

The factors already discussed, high water content and large organ size may cause deterioration resulting in weak and fragile charcoal. Some taxa produce particularly fragile charcoals on charring regardless of the conditions on preservation. The experimentally charred tissues of the root tuber of Erodium glaucophyllum (Plates 21 and 22), the cortex of many aquatic monocotyledonous taxa such as Alisma spp. (Plates 41 to 42), and Typha spp. (Plates 48 and 49) all exemplify this phenomenon.

Such fragile charcoal types, whether or not their condition is induced by a poor environment for preservation, are less likely to survive the post-preservation environment, the processes of recovery and sorting than charcoals of some taxa that are more solid and robust. Deteriorated and fragile charcoals are characterised by soft charred tissues that are easily reduced to a soft fine powder. Such organs and tissues often contain large cavities resulting in narrow regions of tissue forming weak points along which fracturing occurs, eventually reducing the tissue to a mass of unidentifiable fragments.

The post-preservation environment is subject to a range of variables such that it may or may not allow survival of charred organs and tissues, whether these are fragile or

robust as a result of preservation by charring. Several factors involving dispersal after preservation, the environment of deposition, recovery and sorting affect the survival of charred vegetative parenchymatous remains. These can be summarised as follows.

1) Mechanical damage encountered in dispersal from the site of preservation to the site of deposition if these are different.

- trampling, an active process,
- freeze/thaw damage, a passive process.

2) Period of time charred tissues remain exposed.

3) Conditions of the depositional environment,

- weight of material covering remains,
- leaching through the depositional environment,
- physical disturbance.

4) Period of burial.

5) Mechanical damage encountered in recovery and sorting,

- attrition by rubbing against other charred fragments, tools etc. an active process,
- damage caused by wetting and drying during flotation, a passive process.

8.4 'SORTING BIAS'

Despite the numerous ways in which charred vegetative parenchymatous tissues may end up in a deteriorated state, beyond identification or even survival, it is probable that a large proportion of charred 'soft' archaeological tissues do survive to the stage of sorting. Without the means for identification of such a large quantity of material, it is reasonable not to expect the archaeobotanist to spend time sorting for this new class of charred tissues from what really are unidentifiable fragments. In the past large quantities of potentially valuable material will have been discarded together with the ethnobotanical information they embody.

It is at this point that any bias in any inference drawn from the identification of plant remains is likely to emerge. The recognition of charred parenchymatous tissues, simply as a class of remains distinct from seeds, cereal remains and wood, to be isolated and identified is therefore the first step in the elimination of such bias. Distinguishing between identifiable charred vegetative parenchymatous storage tissues, other identifiable plant remains of either similar or different origin is possible under the low power magnifications offered by a binocular reflected light microscope. Identification is however

often not possible without the use of the higher magnifications possible under higher powered epi-illuminated or scanning electron microscopy.

The characters of parenchymatous storage tissues observable using the low magnifications of a binocular reflected light microscope that allow them to be distinguished easily from fragments of wood, seed, dung or unidentifiable charred fragments are detailed below.

- 1) Fragments are often rounded in nature, unless recently fractured, because after preservation sharp corners and protruding tissues tend to become removed cell by cell. This is with the exception of the protrusion of vascular tracts in some instances, that are robust enough to resist this form of surface erosion.
- 2) The cells themselves are visible as being spherical or more or less isodiametric as opposed to being elongated like fibres, tracheids and vessels in wood fragments.
- 3) Tissues are composed of cells with a distinct organization and each cell has a specific relationship with those surrounding it. This is not

relationship with those surrounding it. This is not the case with either charred fragments of human or other animal faeces. These are described in Chapter five.

- 4) Some charred parenchymatous tissues are dull in texture but contain small dense reflective regions representing the charred remains of sclerenchymatous and vascular tissues. Such regions are easily recognisable under low power magnifications.
- 5) Charred vegetative parenchymatous organs often contain either regular or irregular patterns of cavities. These may be of any of several types described in Chapter five.

8.5 THE IDENTIFICATION OF PARENCHYMATOUS VEGETATIVE REMAINS OF PLANT STORAGE ORGANS.

8.5.1 Introduction

Having established that vegetative parenchymatous remains of storage organs form a class of charred tissues that may be distinguished from the remains of other plant organs in the process of sorting, then identification may proceed. Before methods of identification are discussed the nature

of the diagnostic characters and their use in identification will be considered.

The use of diagnostic characters arising as artefacts in identification of charred tissues in combination with other natural characters allows identification to proceed further than would be the case if anatomical and morphological characters were used alone. This is especially true in the case of more deteriorated tissues. While all artifactual characters are important in the ultimate identification of a taxon, three classes of characters feature largely in the processes of identification.

- 1) The presence or absence of cavities in tissues, their type, size, position and orientation.
- 2) The increased thickness of cell walls or the solidification of their contents compared with the preservation of the natural thin walls of parenchyma cells.
- 3) The deterioration of parenchymatous or aerenchymatous tissues to solid or vesicular carbon or to other forms.

8.5.2 The use of diagnostic characters in identification

Using these characters with the more conventional morphological and anatomical characters, groups of taxa, with and without close taxonomic links, may be identified from the wide range of organs and tissues examined in this research. These groups may occur at different levels in the taxonomic hierarchy.

Of the families examined, some, such as the Umbelliferae, the Compositae and the Cyperaceae, are represented here by several taxa each with a similar morphology. Most other families examined are represented by one or two taxa. Groups of taxa within the families with a larger representation, may be recognised by charring in certain common characters or groups of characters in the charred tissues. Charred plant tissues may then be recognised as having characteristics of the charred anatomy of organs of a family or related groups within a family.

8.5.3 Examples of taxa with clear diagnostic characters

The charred anatomy of Daucus carota (Plates 22 to 24), though typical of many fleshy secondary roots, is highly characteristic because of the type of deterioration that occurs on charring is that restricted to the Umbelliferae. This is different in certain respects from the

occurs on charring is that restricted to the Umbelliferae. This is different in certain respects from the deterioration in non-Umbelliferous roots. The roots of Heracleum sphondyllum (Plates 24 to 26), Myrrhis odorata (Plates 26 and 27) and the root tuber of Conopodium majus (Plate 22) all display this type of charred anatomy. Briefly these are a pattern of deterioration caused by the formation of cavities both radiating out from central axis and external to this linear cavities oriented tangentially to the external surface. Tissue between the cavities is often, though not necessarily so, preserved intact.

Within the Compositae, that bear fleshy secondary roots, two groups may be recognised, each with common anatomical characters. The Tragopogon (Plate 40)/Cichorium (Plate 34) type, where the secondary xylem is largely woody, is easily recognised in the charred state. The Anacyclus (Plates 31 and 32)/Inula (Plates 35 and 36)/Saussurea (Plate 36) type is characterised by the slight deterioration of the fleshy root tissues since this is largely prevented by the presence of secretory cavities. Other taxa of Compositae have different charring characters and though these are typical of the individual taxa, they cannot yet be said to be typical for the family or for a group of taxa within the family until a wider range of species has been examined.

Within the Cyperaceae the morphology of storage organs of the taxa under study here varies considerably. In all however the parenchymatous tissues are similar and though the effects of deterioration on these tissues generally may vary, it may be said that these are characteristic of the Cyperaceae. The cells are rounded and circular to ovoid in shape, are either thin or slightly thick walled and generally homogeneous in size throughout the tissue. Schoenoplectus tabernaemontani (Plates 47 and 48) is composed largely of aerenchymatous tissues and does not share this character in common with other members of the Cyperaceae represented here.

8.5.4 Identification of related and unrelated taxa

Distinguishing between closely related taxa is often not possible. For example distinguishing between Alisma plantago-aquatica and Alisma lanceolatum, using either anatomical or morphological characters can be very difficult. In other cases morphological characters alone provide the only way of distinguishing between closely related taxa. If anatomical characters are all that are available then often identification may only be taken to the generic level. This is the case with the rhizome tubers of Cyperus esculentus (Plates 44 and 45) and Cyperus rotundus (Plates 46 and 47) and the roots of

and the stolon tuber of Sagittaria sagittifolia (Plate 42), are easily distinguished using morphological characters, but fragments of charred tissue lacking suitable morphological characters can often not be separated and would therefore only be identified as the 'Alismataceae' type.

Many of the families included in this research are represented by two or more taxa which differ considerably in both anatomy and morphology, and in the effects of charring. In these cases it is not possible to recognise 'natural' groups of taxa with characters in common that would be useful in identification. Asphodelus aestivus, a root, (Plates 56 and 57) and Polygonum X hybridum, a rhizome (Plates 57 and 58) of the Liliaceae, Acorus calamus, a rhizome (Plates 53 and 54) and Arum maculatum, a tuber (Plates 54 and 55) of the Araceae, and Biebersteinia multifida, a swollen root (Plate 21) and Erodium glaucophyllum, a root tuber (plates 21 and 22) of the Geraniaceae, are examples.

Conversely, systematically unrelated taxa may have vegetative organs that are morphologically similar enough, even if only superficially, to cause confusion in identification. Numerous fleshy dicotyledonous roots provide examples as do the rhizomes of Acorus calamus and

provide examples as do the rhizomes of Acorus calamus and Butomus umbellatus (Plates 40 and 41). The latter may be separated under high magnification using anatomical criteria, though in highly fragmented and deteriorated charred tissues even this may present problems.

8.5.5 Non-Vegetative Parenchyma

It has been shown that some non vegetative tissues produce on charring a type of charcoal that is both highly fragile and offers few characters upon which to base an identification. Malus domestica and Ficus carica are examples. The parenchyma of dried fruits with a lower sugar content such as Quercus robur do preserve well and offer anatomical and morphological criteria that would normally allow identification to the level of genus. The parenchyma contained within the Andricus ssp. gall on Quercus robur, though of vegetative origin may be classified in terms of preservation and identification along with the acorn since the results of charring are similar. The parenchyma of the endosperm of cereal caryopses deteriorates completely to a vesicular carbon and so identification of these would have to be based on morphological criteria alone.

8.5.6 Methods of Identification

The identification of vegetative parenchymatous organs may be achieved by the recognition of combinations of morphological, anatomical and artefactual characters common to progressively smaller groups of taxa until the particular combination of characters is possessed by one taxon only. The occurrence and use of artefactual characters, and the deterioration and loss of many classically useful taxonomic characters results in the failure of any system of identification designed to reflect phylogenetic trends. Any system of identification of charred organs therefore has to be wholly artificial in nature.

Different methods have been considered for the identification of the taxa under examination here: written or computerised keys and punched cards. Of these only the written and computerised keys were found to be appropriate for the types of character states of diagnostic value.

For such written keys to be computerised techniques were required that were beyond the range of this project. Punched cards, though quick and easy to use were found to be too limited for the range and number of diagnostic characters it was necessary to use in identification to be

achieved and were therefore rejected. It was decided that at this stage that only written keys would be developed for identification.

8.6 IDENTIFICATION USING A DICHOTOMOUS KEY

The aim of presenting the key below is to demonstrate the high potential for the identification of vegetative parenchymatous storage organ remains and to provide a skeleton upon which to base further information, rather than to provide an exhaustive method for identification for all archaeobotanical remains of this type. It enables 71 taxa to be identified.

The reason for examining a wide range of tissues and organs was to determine the extent to which identification was possible in morphologically and anatomically varied and systematically distant taxa. While, in this respect, a high potential for identification has been demonstrated it must be acknowledged that the key is not exhaustive in the identification of vegetative parenchymatous organs from any particular limited geographical area. Its application however should not be underestimated. A wide range of taxa are covered and there exists the potential for the identification of the organ type regardless of whether the specific taxon is represented in the key or not. Above

all the key demonstrates the use of combinations of the morphological, anatomical and artifactual characters examined in this research, in the identification of vegetative parenchymatous storage organs in general. This may then be viewed as an experimental exercise though with specific applications to particular archaeological situations.

Many of the taxa under examination in this research produce

different results on charring depending on whether the tissues are dried or fresh (wet) on charring, or whether the organ, if large, is whole or fragmented. The remains of some taxa therefore may be represented by several different states of charred tissues. The key has been constructed so that this variation in the charred state is considered. It is however important to understand the nature of the various characters employed before use of the key is attempted. Many of the characters referred to in the key are artifactual rather than anatomical or morphological criteria. It is impractical to expand such characters in the key and so readers are referred to Chapter five for full classification.

A problem with the identification of charred vegetative parenchymatous remains, not present with either seeds,

leaves or wood, is that before an attempt may be made to attach a specific or generic name to a fragment it is often decided what type of organ the fragment is derived from. Even in the rare event of the complete organ surviving it is not always the case that the organ type is immediately obvious.

If possible therefore the first step in identification of either whole or fragmented vegetative parenchymatous storage organs is the determination of organ type. External morphology is often determinable in small organs where complete or at least partial preservation is usually the case. In much larger organs however, such as many secondary roots, large rhizomes such as Nymphaea alba and tubers such as Bryonia dioica and Tamus communis complete preservation or even sufficient partial preservation of the external surface to determine morphology may be very rare.

Identification of charred vegetative parenchymatous remains using the key put forward here may be done on several levels, using different parts of the key depending on the survival of different characters and groups of characters. Some taxa may be identified on morphology alone or on a combination of morphological and anatomical and artefactual characters. If the organ's morphology is

indeterminable identification may proceed on varying levels of combinations of anatomical and artefactual characters. These range from a wide set of characters from different tissues to characters derived from the ground tissue only. In the latter case identification to the 'type' level may only be achieved in many cases. The first steps in the key allow identification to one of thirteen groups representing different morphological and anatomical categories. These are:-

GROUP I	Small tubers
GROUP II	Medium sized tubers
GROUP III	Massive tubers
GROUP IV	Narrow rhizomes
GROUP V	Medium width rhizomes
GROUP VI	Large rhizomes
GROUP VII	Secondary roots (Type 1)
GROUP VIII	Secondary roots (Type 2)
GROUP IX	Tissues with collateral vascular bundles
GROUP X	Tissues with irregularly arranged vascular bundles
GROUP XI	Tissues with amphivasal concentric vascular bundles
GROUP XII	Tissues with amphicribal concentric vascular bundles or meristeles

GROUP XIII Parenchymatous or aerenchymatous tissues
or deteriorated tissues without vascular
or mechanical tissues.

DICHOTOMOUS KEY

- 1 Organ whole or partially so: morphology determinable__2
Organ fragmented: morphology indeterminable_____9
- 2 Organ rounded, elongated and tapering at either end or
massive, but so that any point of attachment is
narrower than the organ's widest point_____3
Organ not as above_____5
- 3 Organ less than 1.5 cm across any axis_____(GROUP I)19
Organ greater than 1.5 cm across any axis_____4
- 4 Organ between 1.5 and 6 cm across 2 or 3 axes or up to
10 cm across one axis (ie elongated)_____(GROUP II)40
Organ greater than 6 cm across any axis_____(GROUP II)61
- 5 Organ elongated alone one axis, length often
indeterminable and more or less rounded in
transverse section, not tapering. Points of
attachment same width as organ. Nodes may be
visible, organ may be branched_____7
Organ elongated along one axis, rounded in transverse
section tapering from one end to the other, nodes
absent, may be branched._____6

- 6 Cavities radiating out from a central axis of the
organ_____ (GROUP VII) 107
No such cavities_____ (GROUP VI) 117
- 7 Organ less than 1.5 cm across in transverse
section_____ (GROUP I) 63
Organ greater than 1.5 cm across in transverse
section_____ 8
- 8 Organ between 1.5 cm and 2.5 cm across in transverse
section_____ (GROUP V) 84
Organ greater than 2.5 cm across_____ (GROUP VI) 97
- 9 Fragment composed of parenchyma with vesicular and
mechanical tissue, with or without cavities_____ 10
Fragment composed of either solid or vesicular carbon
or composed entirely of parenchymatous
tissue_____ (GROUP XII) 154
- 10 Fragment of charred parenchymatous tissue with possible
elongation along one axis. Dicotyostele present
or vascular bundles all parallel and often
orientated along this axis_____ (GROUP II) 63
Fragment of charred parenchymatous tissue without such
orientation, dicotyostele or vascular bundle
arrangement_____ 11

- 11 Fragment of charred parenchymatous tissue containing
obvious vesicular, tension fracture or
secretory cavities_____12
- Fragment of charred parenchymatous tissue without such
cavities_____15
- 12 Cavities elongated and orientated along the long axis
of the fragment or radiating out from a central
point or axis_____13
- Cavities irregular in shape, though generally rounded
and more or less randomly
placed_____(GROUP 1)19
- 13 Cavities radiating out from a central axis or
point_____14
- Cavities often rounded in transverse section though not
necessarily so, but not radiating out from a
central axis or point_____(GROUP IV)63
- 14 Cavities radially elongated in transverse section and
radiating out from a central point within the
organ_____(GROUP 1)28
- Cavities radially elongated in transverse section and
radiating out from a central long axis of the
organ_____(GROUP VII)107

15	Fragment of charred tissue composed of parenchyma, vascular and mechanical tissues with no particular orientation, vascular tissues composed of bundles or meristeles_____	16
	Fragment of charred parenchymatous tissue composed entirely of solid or vesicular carbon or visible parenchyma cells_____	19
16	Vascular bundles collateral_____ (GROUP IX)	132
	Vascular bundles/meristeles other than collateral____	17
17	Vascular bundles of irregular arrangement____ (GROUP X)	144
	Vascular bundles/meristeles of concentric arrangement_____	18
18	Vascular bundles amphivasal_____ (GROUP X)	147
	Vascular bundles/meristeles amhicribal____ (GROUP XI)	149
 GROUP I		
19	Organ whole or partially so: morphology determinable_____	20
	Organ fragmented: morphology indeterminable_____	26
20	Small tuber, more or less spherical, no nodal scars 0.4 to 1.5 cm across_____	26
	Small tuber other than spherical_____	21

- 21 Small tuber, more or less ovoid 0.4 to 1.5 cm
across _____ 22
Small tuber elongated along one axis to length at least
double that of width _____ 25
- 22 Nodal scars absent or indeterminable _____ 23
Nodal scars present _____ 24
- 23 Point of attachment at one end
only _____ Ranunculus ficaria
Points of attachment or buds at either end or over
surface _____ 31
- 24 Ovoid tuber with dormant bud at distal end and rhizome
detachment scar at
proximal end _____ Cyperus esculentus
Ovoid tuber with rhizome detachment scars at distal
and/or proximal ends and over
surface _____ Cyperus rotundus
- 25 Node and bud scars absent, point of attachment at one
end only _____ Ranunculus ficaria
Node and bud scars absent, points of attachment at both
distal and proximal ends _____ Arrhenatherum elatius

26 Tissue deteriorated by the presence of cavities_____	27
No cavities present_____	30
27 Cavities or single cavity compressing all tissues against internal wall of organ or cavities radiating out from a central point within the tuber_____	28
Cavities not as above_____	45
28 Cavities or single cavity compressing all tissues against internal wall of tuber. Tuber hollow_____	<u>Ranunculus ficaria</u>
Cavities radiating out from a central point within the tuber_____	29
29 Compressed tissues between cavities much narrower than cavities themselves, cavities rectangular_____	<u>Lathyrus linifolius</u>
Compressed tissues between cavities as wide as cavities, cavities eliptical_____	<u>Conopodium majus</u>
30 Cavities absent, cells containing starch grains_____	31
Cavities absent, cells devoid of contents_____	33

31 Starch grains ovoid _____ Ranunculus ficaria
Starch grains spherical _____ 32

32 Organ spherical 0.4 to 1.5 cm
across _____ Lathyrus linifolius
Organ morphology indeterminable _____ Lathyrus linifolius/
Withania somnifera

33 Cells thick walled _____ Arrhenatherum elatius
ssp. bulbosum
Cells thin walled _____ 34

34 Cells rectangular to barrel shaped _____ Hordeum bulbosum
Cells not as above _____ 35

35 Cells ovoid _____ Cyperus rotundus/
Cyperus esculentus
Cells not as above _____ 45

GROUP II

36 Organ whole or partially so: morphology
determinable _____ 37
Organ fragmented: morphology
indeterminable _____ 45

37 Organ elongated to several times that of width _____	44
Tuber other than elongated _____	38
38 Nodes present _____	39
Nodes absent _____	42
39 Tuber ovoid _____	40
Tuber other than ovoid _____	41
40 Surface smooth _____	<u>Sagittaria sagittifolia</u>
Surface wrinkled _____	<u>Arum maculatum</u>
41 Tuber spherical or nearly so _____	42
Tuber flattened _____	43
42 Depression in upper surface containing bud scars _____	<u>Crocus sativus</u>
Tuber spherical with no depression _____	45
43 Tuber dorsiventrally flattened _____	<u>Cyclamen persicum</u>
Tuber laterally flattened _____	44
44 Single detachment scar at proximal end _____	<u>Orchis mascula</u>
Detachment scars at both proximal and distal ends _____	<u>Erodium glaucophyllum</u>

45	Whole or fragment of tuber containing cavities _____	46
	Whole or fragment of tuber having no cavities _____	56
46	Cavities radiating out from a single axis or point ____	47
	Cavities irregular and less random _____	48
47	Cavities radiating out from a central point _____	<u>Asphodelus aestivus</u>
	Cavities radiating out from a central point _____	<u>Conopodium majus</u>
48	Parenchyma composed of storied rectangular cells _____	<u>Scorzonera judaica</u>
	Parenchyma cells rounded or deteriorated _____	49
49	Parenchyma cells deteriorated so that their three dimensional shape is not determinable _____	<u>Erodium glaucophyllum</u>
	Parenchyma cells not deteriorated _____	50
50	Parenchyma cells solid _____	51
	Parenchyma cells devoid of contents _____	52
51	Cells angular _____	<u>Orchis mascula</u>
	Cells rounded _____	<u>Arum maculatum</u>

- 52 Cavities spherical or nearly
 so _____ Sagittaria sagittifolia
 Cavities other than this _____ 53
- 53 Cavities linear _____ Crocus sativus
 Cavities irregular or random _____ 54
- 54 Tissue somewhat vesicular _____ Arum maculatum
 Tissue not vesicular - each cell clearly visible _____ 55
- 55 Vascular bundles collateral _____ Cyclamen persicum
 Vascular bundles irregular _____ Alisma spp.
- 56 Parenchyma cells radiating out from a central point and
 packed with rounded starch
 grains _____ Withania somnifera
 Parenchyma cells solid or devoid of contents _____ 57
- 57 Parenchyma cells solid _____ Orchis mascula
 Parenchyma cells devoid of contents _____ 58
- 58 Parenchyma cells square or
 rectangular _____ Scorzonera judaica
 Parenchyma cells rounded or polygonal _____ 59

59 Parenchyma cells rounded tissue somewhat
vesicular_____ Cyclamen persicum
Parenchyma cells polygonal tissue not vesicular_____ 60

60 Vascular budles collateral_____ Scirpus maritimus
Vascular tissue arranged in a polystarch organization
below an endodermis_____ Asphodelus aestivus

GROUP III

61 Tissues almost totally deteriorated by the formation of
large cavities_____ Bryonia dioica
Large cavities not present_____ 62

62 Parenchyma deteriorated and highly vesicular. Vascular
bundles collateral, raphides up to 200 µm long
present_____ Tamus communis
Parenchyma cells determinable. Vascular bundles and
raphides not present. Druses
present_____ Rheum rhaponticum

GROUP IV

63 Organ whole or in large fragments: complete anatomy
determinable_____ 64
Organ in small fragments: complete anatomy
indeterminable_____ 71

64 Vascular tissue arranged in dictyosteles: meristeles	
amphicribally arranged_____	65
Vascular tissue arranged in collateral or amphivasal	
vascular bundles_____	66
65 Vascular tissue arranged in two concentric dictyosteles	
separated by a hollow fibre	
cylinder_____	<u>Pteridium aquilinum</u>
Vascular tissue arranged in a single dictyostele with	
no fibre cylinder_____	<u>Polypodium interjectum</u>
66 Vascular bundles collateral_____	67
Vascular bundles amphivasal or irregular_____	70
67 Endodermis/endodermoid sheath present_____	68
Endodermis/endodermoid sheath not present_____	69
68 Stelar tissue aerenchymatous_____	<u>Butomus umbellatus</u>
Stelar tissue parenchymatous_____	<u>Scirpus maritimus</u>
69 Naturally deteriorated pith	
present_____	<u>Doronicum grandiflorum</u>
Pith not deteriorated_____	<u>Anemone nemorosa</u>
70 Stele and cortex parenchymatous_____	<u>Cyperus longus</u>
Stele and cortex aerenchymatous_____	<u>Acorus calamus</u>

71	Ground tissue indeterminable	<u>Polygonatum X hybridum</u>	
	Ground tissue determinable		72
72	Ground tissue aerenchymatous		73
	Ground tissue parenchymatous		76
73	Aerenchymatous cells packed with starch grains		74
	Aerenchymatous cells devoid of contents but thick walled		75
74	Vascular bundles collateral	<u>Nuphar advena</u>	
	Vascular bundles amphivasal	<u>Acorus calamus</u>	
75	Aerenchyma cells very thick walled but devoid of contents	<u>Butomus umbellatus</u>	
	Aerenchyma not as above		91
76	Cells solid		77
	Cells devoid of contents		78
77	Cells packed with rounded starch grains or if solid starch grains sinuous	<u>Anemone nemorosa</u>	
	Cells solid, cells walls rounded not sinuous	<u>Doronicum grandiflorum</u>	

- 78 Parenchyma associated with collateral, irregular or
concentric vascular bundles_____79
Parenchyma associated with amphi-cribal meristeleles____82
- 79 Vascular bundles, parenchyma cells polygonal and thin
walled_____Scirpus maritimus
Vascular bundles not as above_____80
- 80 Vascular bundles with irregular
arrangement_____Curcuma domestica
Vascular bundles not as above_____81
- 81 Vascular bundles amphivasal_____Curcuma domestica
Vascular tissue not as above_____89
- 82 Meristeleles present, parenchyma cells thin walled____83
Meristeleles present, parenchyma cells
thick walled_____Dryoperis filix-mas
- 83 Meristeleles in transverse section ovoid, long axis
two to five times greater than that of short
axis_____Pteridium aquilinum
Meristeleles more circular in transverse section or if
ovoid long axis less than two times that of
short axis_____Polypodium interjectum

GROUP V

- 84 Organ whole or in large fragments: morphology
determinable_____85
- Organ in small fragments: morphology
indeterminable_____89
- 85 Internodes no more than one and a half times that of
width of rhizome. Rhizome often regularly
branched_____86
- Internodes often greater than one and a half times that
of width of rhizome. Rhizome not highly
branched_____88
- 86 Mid-internodal region as wide as or wider than node:
rhizome circular in transverse
section_____ Alpinia galanga
- Mid-internodal region narrower than node_____87
- 87 Rhizome circular in transverse
section_____ Polygonatum X hybridum
- Rhizome dorsoventrally flattened_____ Zingiber officinale
- 88 Rhizome with nodes wide apart: stelar tissue
aerenchymatous_____ Schoenoplectus tabernaemontani
- Rhizome with nodes wide apart: stelar tissue
parenchymatous_____ Sparganium erectum

89	Fragment of rhizome containing large cavities	90
	Fragment of rhizome without cavities	91
90	Tissues deteriorated beyond that which allows individual cells to be seen	<u>Polygonatum X hybridum</u>
	Tissue containing discernable cells	<u>Zingiber officinale</u>
91	Tissue aerenchymatous, though cells are compressed to form small irregular cavities	<u>Schoenoplectus tabernaemontani</u>
	Tissue parenchymatous	92
92	Parenchymatous ground tissue somewhat vesicular	93
	Parenchymatous ground tissue not vesicular	94
93	Vascular tissue collateral in arrangement and heavily capped with fibres at the xylem pole	<u>Alpinia galanga</u>
	Vascular bundles amphi-cribal and not capped with fibres	<u>Zingiber officinale</u>
94	Parenchyma thin walled	95
	Parenchyma thick walled	96

- 95 Vascular bundles collateral and capped by
 fibres_____ Typha spp.
 Vascular bundles collateral or amphivasal but
 not capped by fibres_____ Cistanche tubulosa
- 96 Vascular bundles collateral, xylem tissue containing
 fibres parenchyma containing
 druses_____ Polygonum bistorta
 Vascular bundles collateral, xylem with few
 fibres_____ Sparganium erectum
- GROUP XI**
- 97 Organ whole or in large fragments: morphology
 determinable_____ 98
 Organ in small fragments: morphology
 indeterminable_____ 101
- 98 Truncated pattern of nodes, petiole and peduncle
 base scars visible_____ 99
 Nodes if present, at least equivalent width of
 rhizome apart_____ 100
- 99 Petiole and peduncle bases forming rounded abscision
 scars in a regular phyllotaxic arrangement_____ 102
 Petiole or peduncle bases without abscision _____ 103

- 100 Nodes present, organ circular in transverse
section_____ Sparganium erectum
- Nodes absent, organ laterally
flattened_____ Polygonum bistorta
- 101 Ground tissue aerenchymatous_____ 102
Ground tissue parenchymatous_____ 103
- 102 Large asterosclereides present_____ Nymphaea alba
Asterosclereides absent_____ Nuphar advena
- 103 Parenchyma cells very thick walled and empty_____ 104
Parenchyma cells thin walled, solid or deteriorated
to vesicular carbon_____ 106
- 104 Vascular tissue arranged in amphi-cribal
meristele_____ Dryopteris filix-mas
Vascular tissue arranged otherwise_____ 105
- 105 Vascular bundles collateral, xylem often containing
many fibres, parenchyma containing
druses_____ Polygonum bistorta
Vascular bundles collateral, xylem without fibres,
parenchyma without druses_____ Sparganium erectum

106 Parenchyma cells thin walled, vascular bundles
collateral or amphivasal _____ Cistanche tubulosa
Parenchyma cells solid or deteriorated to a vesicular
carbon _____ Nymphaea alba

GROUP VII

107 Organ whole or partially so: morphology and complete
tissue organization determinable _____ 108
Organ fragmented: morphology an complete tissue
organization indeterminable _____ 109

108 Root highly ramified _____ Myrrhis odorata
Root unbranched or little branched _____ 109

109 Secretory cavities present _____ 110
Secretory cavities absent _____ 112

110 Secretory cavities present throughout all tissues
of root _____ 111
Secretory cavities restricted to phloem and xylem and
rarely present in outer
parenchyma _____ Inula helenium

- 111 Parenchyma of pith somewhat deteriorated and
 vesicular_____ Saussurea lappa
 Parenchyma of pith wall preserved. Cells thin walled
 and devoid of contents_____ Anacyclus pyrethrum
- 112 Tissues of root divided into obvious regions of xylem
 and phloem_____ 113
 No obvious xylem and phloem regions, radiating
 cavities throughout tissues_____ Asphodelus aestivus
- 113 Tissue of xylem woody_____ 114
 Xylem largely parenchymatous_____ 115
- 114 Radially oriented linear groups of vessels up to five
 cells wide_____ Cichorum intybus
 Radially oriented linear groups of vessels rarely more
 than two cells wide_____ Tragopogon pratensis
- 115 Outer deteriorated tissue of the phloem and pericyclic
 parenchyma vesicular and without large
 tangentially elongated
 cavities_____ Scorzonera hispanica
 Outer deteriorated tissue of the phloem and pericyclic
 parenchyma not vesicular_____ 116

116 Cavities in outer tissue rounded in transverse
section _____ Symphytum officinale

Cavities in outer tissue tangentially

elongated _____ Daucus carota

_____ Myrris odorata

_____ Heracleum sphondylium

GROUP VIII

117 Vascular tissue organized in concentric rings

alternating with cavities _____ Beta vulgaris

ssps. maritima or vulgaris

Vascular tissue arranged differently _____ 118

118 Xylem restricted to a very narrow central tract
containing little parenchyma or deteriorated

parenchyma _____ 119

Xylem tissue woody or parenchymatous but at least as

wide as phloem tissue or wider _____ 120

119 Xylem forming solid central tract. Phloem and
pericyclic parenchyma containing tangentially
elongated parenchyma _____ Taraxacum officinale

Xylem largely deteriorated. Phloem and pericyclic

parenchyma without cavities _____ Potentilla anserina

120 Xylem woody _____ 121

- 125 Xylem composed of concentric rings of bundles of vessel elements embedded in a parenchymatous ground tissue composed of solid cells _____ Biebersteinia multifida
- Xylem not as above, ground tissue often solid carbon cell boundaries not being visible _____ 126
- 126 Root up to five cm wide and sharply tapering over a length of up to 20 cm _____ Crambe cordifolia
- Root no more than 1.5 cm wide and not tapering sharply _____ Crambe maritima
- 127 Distinct cavities in pith, rounded in transverse section and elongated longitudinally. Druses present _____ Eryngium maritimum
- Cavities in any tissues, few. Druses absent _____ 128
- 128 Junction between phloem parenchyma and the tissue of the xylem marked by a relatively wide region of solid carbon resulting from the deterioration of the phloem _____ Gentiana lutea
- No such junction existing _____ 129

129 Phloem parenchyma square or rectangular in
transverse and longitudinal

section Scorzonera schweinfurthii

Phloem parenchyma not as above 130

130 Phloem parenchyma rounded in transverse section but
elongated and storied in longitudinal

section Arctium minus

Phloem parenchyma not as above 131

131 Phloem parenchyma polygonal to rounded and somewhat
irregular in organization in both transverse and
longitudinal section Raphanus sativus

Parenchyma vesicular Arctium minus

GROUP IX

132 Ground tissue aerenchymatous 133

Ground tissue parenchymatous 134

133 Aerenchyma cells packed with starch

grains Nuphar advena

Aerenchyma cells compressed into flat

plates Schoenoplectus tabernamontani

- 134 Parenchyma cells packed with rounded starch grains _____ Anemone nemorosa
 Parenchyma cells without starch grains _____ 135
- 135 Parenchyma cells composed of solid carbon _____ 136
 Parenchyma cells vesicular or devoid of contents _____ 137
- 136 Cell walls sinuous with distinct intracellular air spaces circular in transverse section _____ Anemone nemorosa
 Cell walls generally rounded with no air spaces _____ Doronicum grandiflorum
- 137 Parenchymatous ground tissue deteriorated to vesicular carbon _____ 138
 Ground tissue not deteriorated _____ 139
- 138 Raphides present in ground tissue. No fibres associated with vascular bundles _____ Tamus communis
 No raphides present. Vascular bundles having prominent fibre cap at xylem pole _____ Alpinia galanga
- 139 Parenchyma cells thin walled _____ 140
 Parenchyma cells thick walled _____ 141

140 Druses present _____ Polygonum bistorta
Druses absent _____ 142

141 Cells irregularly organized in transverse
section _____ Sparganium erectum
Cells rectangular and regularly storied in
transverse section _____ Hordeum bulbosum
Arrhenatherum elatius ssp. bulbosum

142 Vascular bundles large and extending into the
parenchymatous ground tissues _____ Cyclamen persicum
Vascular bundles forming discrete tissues apart
from the ground tissue _____ 143

143 Fibre sheath surrounding vascular bundle _____ Typha spp.
Scirpus maritimus
Fibre sheath absent _____ Cistanche tubulosa

GROUP X

144 Irregular vascular bundles embedded in aerenchyma
composed of very thick walled cells circular
intransverse section _____ Butomus umbellatus
Tissues not as above _____ 145

145 Irregular vascular bundles embedded in partially
deteriorated ground tissue containing
cavities _____ Sagittaria sagittifolia

Irregular vascular bundles embedded in an
undeteriorated thin walled parenchymatous
ground tissue _____ 146

146 Vascular bundles no more than 120 μ m
across _____ Curcuma domestica

Vascular bundles oftne up to 400 μ m
across _____ Alisma spp.

GROUP XI

147 Vascular bundles embedded in aerenchymatous tissue
packed with starch grains _____ Acorus calamus
Tissues not as above _____ 148

148 Vascular bundles embedded in thin cell walled
ground tissue _____ Alisma spp.

_____ Cistanche tubulosa
Vascular bundles embedded in solid or thick walled
ground tissue _____ Cyperus spp.

GROUP XII

149 Vascular bundles embedded in aerenchyma composed of
very thick walled cells circular

in transverse section Butomus umbellatus

Tissues not as above _____ 150

150 Vascular bundles embedded in partially deteriorated
ground tissue containing

cavities Sagittaria sagittifolia

Zingiber officinale

Tissues not as above _____ 151

151 Ground tissue thick walled with no cavities, vascular
bundles deteriorate to leave hollow channels with
discernable xylem elements but no

phloem Crocus sativus

Tissues not as above _____ 152

152 Meristeles with long axes at least three times longer
than short Pteridium aquilinum

Tissues not as above _____ 153

153 Meristeles rounded and embedded in a ground tissue
with thick cell walls Dryopteris filix-mas

Meristeles rounded and embedded in a ground tissue
with thin cell walls Polypodium interjectum

GROUP XIII

- 154 Discernable cellular structure visible, cells solid or
with or without contents. Cells may be compressed
but cell boundaries still visible_____155
Discernable cellular structure not visible. Charcoal
vesicular, distorted by cavities or solid_____168
- 155 Cells composed of solid carbon_____156
Cells with or without contents but lumen visible____158
- 156 Cells compressed forming the walls of large
cavities_____ Lathyrus linifolius
Cells not compressed_____157
- 157 Cell walls sinuous_____ Anemone nemorosa
Asphodelus aestivus
Orchis mascula
Cells circular or rounded_____ Nymphaea alba
Arum maculatum, Orchis mascula,
Cyperus rotundus, Cyperus esculentus,
Doronicum grandiflorum
- 158 Visible cell structure aerenchymatous_____159
Visible cell structure parenchymatous_____161

159 Aerenchymatous tissue compressed forming the walls of
large cell-like structures, their lumen being the
previous intercellular air space_____ Alisma spp.

Schoenoplectus tabernaemontani

Aerenchymatous tissue not compressed_____ 160

160 Starch grains present_____ Acorus calamus

Nuphar advena

Starch grains not present_____ Nymphaea alba

Butomus umbellatus

161 Parenchymatous cells very thick walled___ Crocus sativus

Dryopteris filix-mas, Polygonum bistorta,

Inula helenium, Arrhenatherum elatius ssp. bulbosum

Cyperus rotundus, Cyperus esculentus,

Sparganium erectum, Crambe maritima

Parenchyma cells with thin walls_____ 162

162 Cells rounded in section_____ 163

Cells other than rounded in section_____ 164

- 163 Cells containing starch grains _____ Anemone nemorosa
Crambe maritima, Arum maculatum
 Starch grains not preserved _____ Pteridium aquilinum
Cyclamen persicum, Cistanche tubulosa,
Curcuma domestica, Doronicum grandiflorum,
Alisma spp., Cyperus rotundus, Cyperus esculentus,
Scorzonera judaica, Scorzonera schweinfurthii,
Zingiber officinale, Arum maculatum,
Hordeum bulbosum, Asphodelus aestivus, Cyperus longus
- 164 Cells polygonal in section _____ 165
 Cells square or rectangular in section _____ 167
- 165 Starch grains not preserved _____ Polypodium interjectum
Typha spp., Beta vulgaris,
Beta vulgaris ssp. maritima
Asphodelus aestivus, Scirpus maritimus
 Starch grains preserved _____ 166
- 166 Starch grains rounded _____ Withania somnifera
 Starch grains ovoid _____ Ranunculus ficaria

167 Starch grains not

preserved _____ Beta vulgaris ssp. vulgaris

Potentilla anserina, Arctium minus

Daucus carota, Pastinaca sativa,

Symphytum officinale, Scorzonera judaica,

Scorzonera schweinfurthii, Hordeum bulbosum

Starch grains preserved _____ Lathyrus linifolius

Withania somnifera

168 Cellular structure deteriorated to more or less solid
carbon though small vesicles or larger

cavities may exist _____ 169

Cellular deterioration but not as above _____ 170

169 Raphides present _____ Asphodelus aestivus

Raphides absent _____ Asphodelus aestivus

Crambe maritima, Crambe cordifolia,

Biebersteinia multifida, Orchis mascula

170 Deterioration vesicular and of 'Tamus' type _____ 171

Deterioration not of this type _____ 172

171 Raphides present _____ Tamus communis

Raphides not present _____ Nymphaea alba, Alpinia galanga

172 Deterioration of 'Rheum' type _____ Rheum rhaponticum

Rheum palaestinum

Deterioration not of this type _____ 173

173 Deteriorated cellular structure composed of thick walled vesicles and small regions of solid carbon and possibly large cavities _____ Ranunculus ficaria,

Bryonia dioica, Brassica campestris,

Arctium minus, Conopodium majus,

Daucus carota, Saussurea lappa,

Scorzonera hispanica, Zingiber officinale,

Arum maculatum, Crocus sativus,

Polygonatum X hybridum, Orchis mascula

Deteriorated cellular structure composed of thin walled broken cellular remains with tension fracture cavities _____ Daucus carota,

Symphytum officinale

Anacyclus pyrethrum, Arctium minus,

Taraxacum officinale, Crocus sativus,

Zingiber officinale

8.7 APPLICATIONS AND LIMITATIONS

The research presented here has demonstrated that the identification of charred vegetative parenchymatous remains is possible often down to the level of species. While this in itself offers enormous potential for archaeobotany in general two specific areas of application should be discussed.

Fistly, the use of these methods, together with a wide range of comparable methods for the identification of other plant tissues and organs, including seeds, cereal remains, wood and pollen, will achieve a more complete record of plant remains from a site. The greater the proportion of the plant remains recovered from a site that are identified the less potentially biased any inference drawn from them will be. The proportion of vegetative parenchymatous remains recovered will vary from site to site. Where, however, charred vegetative parenchymatous tissues form only a minor proportion of the plant remains recovered it may be thought that their identification is also of minor importance. In such cases the relatively time consuming and often costly identification of these tissues may be thought to be impractical. Vegetative parenchymatous tissues will, though, form large proportions of the plant remains recovered from some sites. In these cases their identification, though time

consuming and expensive compared with the identification of other plant remains, will contribute valuable information to the archaeobotany of the site. Sites offering such charred remains may be rare in areas where agriculture is seed based unless there were frequent famine years. Sites of pre-agrarian plant use in these areas however, do hold the potential for the recovery of these types of plant remains. Both new and old world tropical agriculture and temperate and cool temperate Andean agriculture also hold great potential for this class of plant remains.

Secondly, the identification of vegetative parenchymatous tissues may, in certain instances be of use in answering certain archaeological questions as well as providing data for the general build up of information from a site. Vegetative parenchymatous foods and, to a much lesser extent, taxa with other uses, in these cases will have played an important role in the agrarian or pre-agrarian economies of such sites. The role of the major 'root and tuber' staple crops, their origin, cultivation, domestication, and associated agricultural practices in new and old world tropical and temperate and cool temperate Andean regions could be examined in great detail if it were possible to identify their charred remains. This now seems a distinct possibility.

The number of identified charred archaeological remains of many of the important tropical 'root and tuber' crops, such as the yams (Dioscorea spp.), taro (Colocasia esculenta) and sweet potato (Ipomoea batatas), is strikingly low. The charred remains that have been recovered and identified, such as that of Ipomoea batatas by Rosendhal and Yen (1971), are often complete or almost so and usually well preserved. It is likely therefore that the low number of identifications of such remains is due to the lack of known diagnostic criteria useful in the identification of fragmented organs rather than their infrequent occurrences in archaeological deposits. This research has demonstrated that criteria for the identification of fragmented charred remains of such organs and tissues are available and so the potential for a greater number of identifications is high.

Although there is great potential for the application of this research there are also several limitations presented by both the research and areas of its application. The aims of this research and the finite time in which it had to be completed have meant that only a limited number of taxa have been examined. However the range of taxa that have been examined is wide and adequately meets the aims of this research.

While it is true that the use of scanning electron microscopy limits the application of this research to the

well equipped laboratory, the availability of such techniques is becoming more frequent. It is hoped that scanning electron microscopy, as a technique for examining archaeological plant remains under high magnification, will be used to its full potential in the future rather than given the occasional use it receives at the present.

The results of this research and the discussion of the methods of identification show that a wide taxonomic, anatomical and morphological range of taxa will, in the charred state, display various diagnostic characters that may be used in their identification. It has been adequately demonstrated therefore that there is the high potential form the successful identification of charred vegetative parenchymatous storage organs.

8.8 CONCLUSIONS

- 1 Valuable information concerning archaeological sites may be lost, resulting in a biased inference drawn from the botanical remains recovered, due to the inability of the archaeobotanist to identify charred fragments of vegetative parenchymatous storage organs.
- 2 A classification of vegetative parenchymatous storage organs, based on both anatomy and morphology has been developed in an effort to standardise the

terminology used by archaeobotanists to describe such organs.

- 3 The examination of a wide range of experimentally charred vegetative parenchymatous storage organs has shown them to display various diagnostic characters that may be used in their identification.
- 4 Both classical anatomical and morphological characters, and characters resulting from the effects of charring may be used in identification.
- 5 Character states vary according to both water content prior to charring and the size of the fragment of tissue on charring.
- 6 The examination of the diagnostic characters useful in identification of these types of tissues and organs is achieved to the greatest effect by using scanning electron microscopy.
- 7 It is possible to distinguish between the vegetative parenchymatous remains of storage organs and charred non vegetative parenchyma derived from fruits, seeds and associated structures.
- 8 It is often possible to identify the charred remains of vegetative parenchymatous storage organs, using the characters outlined in this research, and so it is important that such tissues are recognised at the stage of sorting plant remains into different categories.

REFERENCES

- Aeschimann, D., 1980 Bocquet G. Allorhizie et homerhizie, une reconsideration des definitions et de la terminologie. Candollea 35, 19-35
- Allison, J., 1949 Godwin, H. Bronze age Plant Remains from Wiltshire. Data for the study of Post-Glacial History. XII. New Phytologist 48, 253-254
- Arber, A. 1920 'Water Plants' - A study of Aquatic Angiosperms. Cambridge University Press
- Armstrong, W. 1972 A re-examination of the functional significance of Aerenchyma. Physiologia 27, 173-177
- Artschwager, E.F. 1924 Studies on the Potato tuber. Journal of Agricultural Research 27, 809-833

- Artschwager, E.F. 1925 Dictionary of Botanical
Equivalents Baltimore Williams
and Watkins
- Artschwager, E.F. 1926 The anatomy of the Vegetative
Organs of the Sugar Beet.
Journal of Agricultural
Research 35, 143-176
- Atal, C.K., 1961 ASCHAGANDHA - An ancient
Schwartz, A.E. Indian drug Economic Botany
15, 256-263
- Ayensu, E.S. 1972 Anatomy of the Dicotyledons.
IV Dioscoreales. General
Editor: C.R. Metcalfe.
Cambridge University Press
- Bailey, C., 1981 Beduin plant utilization in
Danin, A. Sinai and Negev. Economic
Botany 32(2) 145-162
- Baillon, H. 1878 The Natural History of Plants.
(Translated by M.M Hartog) 8
volumes London

- | | | |
|--------------|------|--|
| Bakels, C. | 1988 | Hekelingen, a Neolithic site in the swamps of the Maas estuary. In: U. Körbe Grohne (ed.) <u>Der prähistorische Mensch und seine Umwelt</u> . Stuttgart: C. Konrad Theiss Verlag |
| Banga, O. | 1957 | Origin of the European Cultivated Carrot - The development of the Original European Carrot Material. <u>Euphytica</u> <u>6</u> , 64-76 |
| Barnes, W.C. | 1936 | Effects of some environmental factors on growth and colour of carrots. <u>Cornell University Agricultural Experimental Station. Memoir.</u> <u>186</u> , 1-36 |
| Bell, A.D. | 1979 | The hexagonal branching patterns of rhizomes of <u>Alpinia speciosa</u> L. (Zingiberaceae). <u>Ann. Bot.</u> <u>49</u> , 202-223 |

- | | | |
|-------------------------------|------|---|
| Bell, A.D. | 1980 | The vascular pattern of a
Rhizomatous Ginger (<u>Alpinia
speciosa</u> L. Zingiberaceae) 2.
Rhizome. <u>Ann. Bot.</u> <u>46</u> 213-220 |
| Bell, A.D.
Shirreffs, D.A. | 1984 | Rhizome growth and clonol
development in <u>Amemone
nemorosa</u> L. <u>Ann. Bot.</u> <u>54</u> , 315-
324 |
| Bernhardi, J.J. | 1805 | <u>Beobachtungen über</u>
<u>Pflanzengefäße.</u> Erfurt |
| Berthold, G. | 1886 | <u>Studien über</u>
<u>Protoplasmamechanik.</u> Leipzig |
| Bischoff, G.W. | 1833 | <u>Handbuch der botanischen</u>
<u>terminologie.</u> Nuremburg Schray |
| Bois, D. | 1893 | <u>Dictionnaire d'horticulture</u>
<u>illustré.</u> Paris Irlintrsleck |
| Bois, D. | 1927 | <u>Plantes alimentaires.</u> Paris
Paul Lechevalier |

- Brandenburg, W.A. 1981 Possible Relationships between Wild and Cultivated carrots (Daucus carota L.) in the Netherlands. Kulturpflanze 29, 369-375
- Campbell, G.K.G. 1976 Sugar Beet. In Evolution of Crop plants. N.W. Simmonds. (ed.). 25-28 Longman. London
- Cannon, W.A. 1949 A tentative classification of root systems. Ecology 30, 542-648
- Clausen, J, 1940 Experimental studies on the Nature of species i) The effect of varied environments on Western Northern American Plants. Carnegie Inst. of Washington Publication 520, 1-452 Washington DC
- Keck, D.D.,
- Heisey, W.M.

- | | | |
|-----------------------------------|------|---|
| Cohen, M.N. | 1972 | Some problems in the quantitative analysis of vegetable refuse illustrated by a Late Hnzen site on the Peruvian Coast. <u>Nawpa Pacha</u> <u>10-12</u> , 49-60 |
| Cohen, M.N. | 1978 | Archaeological plant remains from the central coast of Peru. <u>Nawpa Pacha</u> <u>16</u> , 23-50 |
| Cook, C.D.G. | 1968 | Phenotypic Plasticity with Particular Reference to three amphibious plant species. In: V.H. Heywood (ed.) <u>Modern Methods in Plant Taxonomy</u> . 97-111 Academic Press London/New York |
| Cooper, M.R.
and Johnson, A.W. | 1984 | <u>Poisonous plants in Britain their effects on animals and man</u> . Reference Book 161 London HMSO |
| Coursey, D.G. | 1967 | <u>Yams</u> . London Longmans |

- | | | |
|-----------------|------|--|
| Courter, J.W. | 1969 | Historical Notes on Horse |
| Rhodes, A.M. | | Radish. <u>Economic Botany</u> <u>23</u> , |
| | | 156-164 |
| Culpepper, N. | 1669 | <u>The English Physitian</u> |
| | | <u>Enlarged</u> . London |
| Curtis, W.M. | 1940 | The structure and development |
| | | of some apomicts of <u>Taraxacum</u> . |
| | | <u>Kew Bull.</u> <u>1</u> , 1-29 |
| Cutter, E.G. | 1957 | Studies of Morphogenesis in |
| | | Nymphaeaceae 1: Introduction - |
| | | some aspects of the morphology |
| | | of <u>Nuphar lutea</u> (L.) Sm. and |
| | | <u>Nymphaea alba</u> L. <u>Phytomorph</u> <u>7</u> , |
| | | 45-56 |
| Darlington, C.D | 1955 | <u>Chromosome Atlas of Flowering</u> |
| Wylie, A.P. | | <u>Plants</u> . 2nd edition London |
| | | Allen and Unwin |
| Davis, C.H. | 1942 | The response of <u>Cyperus</u> |
| | | <u>rotundus</u> L. to 5 moisture |
| | | levels. <u>Plant Physiol.</u> <u>16</u> , |
| | | 313-316 |

- de Bary, A. 1884 Comparative Anatomy of the vegetative organs of the phanerogams and ferns.
Oxford Clarendon Press
- de Candolle, A. 1835 Introduction a l'étude de la Botanique. VI Paris
- de Candolle, A. 1880 La Phytographie. Paris Masson
- de Candolle, A. 1880 The Origin of Cultivated Plants.
Hafner Publishing Co. New York
(1959 edition, reprint of 2nd edition 1886)
- de Candolle, A.P. 1827 Organographie vegetale.
Peterville Paris
- de Candolle, A.P. 1844 Théorie de la feuille. Arch. et Sci. de la Bibl. Universelle 32,
32-64

- Dennfer, Von. 1978 Chapter 1, p 9-212 In: E. Strasburger (ed.) Lehrbuch der Botanik fur Hochschulen 31st edition Stuttgart Gustav Fischer Verlag
- Dodd, J.D. 1955 An approximation of the minimal tetrakaidecahedron. Am. J. Bot. 42, 566-569
- Donkin, R.A. 1970 Pre Colombian field implements and their distribution in the highlands of Middle and South America. Anthropos 65, 505-529
- Du Chartre, P. 1867 Elements de Botanique. Paris
- Du Reitz, G.E. 1931 Life forms of terrestrial flowering plants. Acta Phytogeogr. Suec. 3(1) 95
- Eldin, H.C. 1951 British Plants. London
- Erichsen-Brown, C. 1979 The use of plants for the past 500 years. Aurora Ontario: Breezy Craks Press

- Errera, L. 1887 Uber Zellenformen und
Seifenblasen Tageblat.
Naturfercher V. Aertze um
Wiesbaden: 246-249
- Esau, K. 1940 Developmental anatomy of the
fleshy storage organs of Daucus
carota. Hilgardia 15, 175-226
- Ervin, E.L. 1970 Observations on sieve elements in
Evert, R.F three perennial monocotyledons.
Am. J. Bot. 57, 218-224
- Felger, R.S. 1985 People of the Desert and Sea -
Moser, M.B. Ethnobotany of the Seri Indians.
University of Arizona Press
- Ford-Lloyd, B.V. 1975 A Revision of Beta section
Williams, J.T. vulgares with new light on the
origin of Cultivated beets. Bot.
J. Lin. Soc. 71, 89-102
- Foster, A.S. 1974 Comparative Anatomy of Vascular
Gifford, E.M. Plants. Freeman and Co. San
Fransisco 2nd edition

- Fritch, F.E. 1903 The Use of Anatomical Characters
for Systematic Purposes. New
Phytol. 2, 177
- Garg, D.K. 1967 Rhizome differentiation in Yellow
Bendixen, L.E. Nut Sedge. Weed Sci. 15, 124-128
Anderson, S.R.
- Gatin, D.C. 1924 Dictionnaire aide-memoire de
botanique. Lechevalier Paris
- Gerrard, J. 1633 The Herbal or Generall Historie
of Plantes. (Enlarged and emended
by Thomas Johnson)
- Gray, A. 1879 The botanical textbook Part I
Standard Botany. (6th edition)
Wilson New York
- Grieve, M. 1931 A Modern Herbal. London Penguin
Books

- Grew, N. 1682 The Anatomy of Plants. Johnson
Reprint Corp. New York and London
(1965)
- Guest, E. 1933 Notes on Plants and Plant
Products with their Colloquial
Names in Iraq. Baghdad
- Guest, E. 1966 Flora of Iraq. Vols 1-4, 8-9,
Al Rawi, A. Baghdad Ministry of Agriculture
Townshend, C.C.
- Hacket, A.C. 1927 Observations on the tubercles of
Ranunculus ficaria L. Ann. Bot.
41, 731-753
- Harris, D.R. 1969 Agricultural systems, ecosystems
and the origins of agriculture.
In: P.J. Ucko and G.W. Dimbleby
(eds.) The domestication and
exploitation of plants and animals.
London Duckworth & Co.
- Harris, D.R. 1972 The origin of agriculture in the
tropics. American Scientist 60,
180-193

- Harris, D.R. 1977 Alternative Pathways toward
Agriculture. In: C.A. Reed (ed.)
Origins of agriculture. The Hague
Mouton
- Havis, L. 1935 The anatomy and histology of the
transition region of Tragopogon
porrifolius. J. Agr. Res. 51, 643-
654
- Havis, L. 1939 Anatomy of the hypocotyl and
roots of Daucus carota. J. Agr.
Res. 58, 557-564
- Hawkes, J.G. 1969 The Ecological Background to
Plant Domestication. In: P.J.
Ucko and G.W. Dimbleby (eds.) The
domestication and exploitation
of Plants and Animals. London
Duckworth and Co.

- Hawkes, J.G. 1986 The Domestication of S. American
Roots and Tubers. In: Recent
Advances in the Understanding of
Plant Domestication and Early
Agriculture. Allen and Unwin
- Hayden, A. 1919 The Ecological Subterranean
Anatomy of Some Plants of a
Prairie Province in central Iowa.
Am. J. Bot. 6(3), 87-105
- Hayward, H.E. 1938 The Structure of Economic Plants.
The MacMillan Co. New York
- Hedrick, V.P. 1919 Sturtevant's notes on edible
plants. State of New York - Dept.
of Agric. 27th Ann Rpt. Vol 2 II
Albany J.B. Lyon Co.
- Heslop, D.H. 1987 The excavation of an Iron age
Settlement at Thorpe Thewls,
Cleveland 1980-1982. CBA Research
Report 65
- Heywood, V.H. 1978 Flowering Plants of the World.
Oxford University Press

- Higinbotham, N. 1942 The three-dimensional shapes of undifferentiated cells in the petiole of Angiopteris erecta. Am. J. Bot. 29, 851-858
- Hillman, G.C. 1978 The origins of Domestic Rye Secale cereale: The finds from Aceramic Can Hasan III in Turkey. Anatolian Studies 28, 157-174
- Hillman, G.C. 1981 Reconstructing Crop Husbandry Processes from charred remains of crops. In: R. Mercer (ed.) Farming Practices in British Prehistory. Edinburgh University Press
- Hillman, G.C. 1985 The Use of Electron Spin
Robbins, C.V. Resonance Spectroscopy to
Oduwale, O. determine the Thermal Histories
Sales, K.D. of Cereal Grains. J. Arch.
McNeil, D.A.C. Sci. 12, 49-58

- Hillman, G.C. 1988 Wild Plant foods and diet at late
 Madyeska, E. Palaeolithic Wadi Kubbaniye -
 Hather, J.G. Evidence from charred remains.
 In: F. Wendorf, R. Shield, A.
 Close (eds.) The Prehistory of
 Wadi Kubbaniye Vol 2, Studies in
 late Palaeolithic Subsistence
 Dallas Southern Methodist
 Universtity Press
- Holm, T. 1929 The application of the term
 rhizome. Rhodora 31, 6-17
- Hooke, R. 1665 Micrographia London
- Hopf, M. 1955 Formveränderungen von
 Getreidekornen beim Verkohlen.
 Ber. der Deutschen Bot.
 Gezellsch. 68, 191-193
- Hubbary, R.L. 1944 The Influence of Air Spaces on
 the 3 dimensional shapes of cells
 in Elodea stems, and a comparison
 with pith cells of Atlantis. Am. J.
 Bot. 31, 561-580

- Hubbary, R.L. 1948 Three dimensional cell shape in the
tuberous roots of Asparagus and
in the leaf of Rhoeo. Am. J. Bot.
35, 558-566
- Jackson, B.D. 1928 A Glossary of Botanic Terms.
Hafner Publishing Co. Inc. New
York
- Johns, C.A. 1870 In: J. Lindley and T. Moore The
Treasury of Botany. (2 Vols.)
London
- Johnson, C.P. 1862 Useful plants of Great Britain.
London Robert Hardwicke
- Kieser, D.G. 1815 Grundzüge der Anatomie der
Planzen. Elemente der phytonomie
erster theil. Phytonomie Jena
- Kelvin, L. 1887 On the division of space within
the minimum partitional area.
Phil. Mag. 24, 503-514
- Knobloch, I.W. 1954 Developmental anatomy of chicory -
the root. Phytomorphology 4, 47-54

- Körber-Grohne, U. 1987 Nutzpflanzen in Deutschland
Kulturgeschichte und Biologie.
 Konrad Thesis Verlag Stuttgart
- Korn, R. 1975 The geometry of plant epidermal
 cells. New Phytol. 72. 1357
- Korn, R.W. 1974 The 3D shape of plant cells and
 Spalding, R. its relationship to pattern of
 tissue growth. New Phytol. 73,
 927-935
- Lewis, F.T. 1923 The typical shape of polyhedral
 cells in vegetable parenchyma and
 the restoration of that shape
 following cell division.
Proc. Amer. Acad. Arts and Sci.
58, 537-552
- Lewis, F.T. 1925 A further study of the polyhedral
 shapes of cells. Proc. Amer.
Acad. Arts and Sci. 61, 1-34

Lewis, F.T.	1928	The shape of cork cells: A simple (a) demonstration that they are tetrakadecahedral. <u>Science</u> <u>69</u> , 625-626
Lewis, F.T.	1928	The correlation between cell (b) division and cell shapes and sizes of prismatic cells in the epidermis of <u>Curcumis</u> . <u>Anot.</u> <u>Rec.</u> <u>38</u> , 341-376
Lewis, F.T.	1930	A volumetric study of growth and cell division in two types of epithelium and the longitudinally prismatic epidermal cells of <u>Tradescantia</u> and the radially prismatic epidermal cells of <u>Curcumis</u> . <u>Anot.Rec.</u> <u>47</u> , 59-99
Lewis, F.T.	1943	A geometric accounting for the diverse shapes of 14-hedral cells: the transition from dodecahedra to tetrakaidecahedra. Am. J. Bot. 30, 74-81

- Lewis, F.T. 1945 The geometry of growth and cell
division in epithelial mozaics.
Am. J. Bot. 30, 766-776
- Lewis, F.T. 1944 The geometry of growth and cell
division in columnar parenchyma.
Am. J. Bot. 31, 619-629
- Lewis, F.T. 1946 The shape of cells as a
mathematical problem. Am. Sci.
34, 359-369
- Lieu, S.M. 1979 Growth forms in the Alismatales I
Alisma trivale and species of
Sagittaria with upright
vegetative axes. Can. J. Bot.
57(3), 2325-2352
- Lieu, S.M. 1979 Growth forms in the Alismateles
II two rhizomatous species:
Sagittaria lancefilia and Butomus
umbellatus. Can. J. Bot. 57(3),
2353-2573
- Lindley, J. 1832 An introduction to Botany.
London Longman

- Lindley, J. 1846 The vegetable kingdom; or, the structure, classification and uses of plants, illustrated upon the Natural System. London
- Mackevic, V.I. 1929 The carrot of Afghanistan. Bull. appl. Bot. Genet. Pl. Br. 20, 517-557
- Manglesdorf, P.C. 1971 Origins of Agriculture in Middle America. In: S. Struever
Macneish, R.S. Prehistoric Agriculture Natural History Press: American Museum
Willey, G.R. Science Books in Anthropology
- Martins, R. 1976 New Archaeological Techniques for the Study of Ancient Root Crops in Peru. Unpublished PhD Thesis
Birmingham University
- Marvin, J.W. 1939 The shape of compressed lead shot and its relation to cell shape.
Am. J. Bot. 26, 280-288

- Marvin, J.W. 1939 A new method for the construction
Matzke, E.B. of three dimensional cell models.
Am. J. Bot. 26, 101-103
- Matzke, E.B. 1939 Volume-shape relationships in
lead shot and their bearing on
cell shapes. Am. J. Bot. 26, 288-
293
- Matzke, E.B. 1946 The three dimensional shape of
bubbles in foam - an analysis of
the role of surface forces in
three dimensional cell shape
determination. Am. J. Bot. 33,
58-80
- McConnel, U. 1957 Myths of Mungkan. Melbourne
University Press, London and New
York, Cambridge University Press
- McQuitty, A. 1984 An ethnographic and
archaeological study of clay
ovens in Jordan. Ann. Dept. Ant.
Amman 28, 259-268
- McQuitty, A. Charred remains from clay ovens
Hather, J.G. in Aqaba. Levant Forthcoming

- Medsger, O.P. 1939 Edible wild plants. New York The
Macmillan Co.
- Metcalfe, C.R. 1950 Anatomy of Dicotyledons. Oxford
Chalk, L. University Press
- Miller, L. prep A study of use of wild plant
El-Azm, A. foods by the Bedouin of Jordan
and Syria.
- Mirbel, C.F.B. 1802 Traité d' anatomie et de
physiologie vegetales. Volume 1
Paris
- Mirbel, C.F.B. 1815 Elements de Physiologie vegetale et
Botanique. Paris
- Morton, J.F. 1963 Principal wild food plants of the
United States excluding Alaska
and Hawaii. Economic Botany 17,
319-330
- Morton, J.F. 1975 Cattails (Typha spp.) - Weed
problem or potential crop.
Economic Botany 29, 7-29

- Mueller, F. 1891 Select extra tropical plants, readily eligible for industrial culture or naturalization, with indications of their native countries and some of their uses.
8th edition Melbourne
- Norton, H. 1981 Plant use in Kaigani Haida culture: correction of an ethnohistorical oversight.
Economic Botany 35(4), 434-439
- Norton, H. 1979 Evidence for bracken as a food from aboriginal peoples of western Washington. Economic Botany 33, 384-396
- Nilsson, N.Hj. 1882 Dikotyla jordstammar. Acta. Univ. Lond. 19
- O'Connell, J.F. 1983 Traditional and modern plant use
Catz, P.K. among the Alyawara of Central
Barnett, P. Australia. Economic Botany 37(1),
80-109

- Ogura, Y. 1972 Comparative anatomy of vegetative organs of the Pteridophytes.
Handbuch der pflanzenanatomie. VII
3 Berlin
- Olsson, G. 1954 Crosses between Brassica napus and Japanese Brassica napella.
Hereditas 40, 249-252
- Parrington, M. 1978 The excavation of an Iron Age Settlement, Bronze age ring ditches and Roman features at Ashville Trading Estate, Abingdon, Oxfordshire. CBA Report 28 Oxford Arch. Report 1
- Patterson, T.C. 1968 Late preceramic and early ceramic cultures of the central coast of Peru. Nawpa Pacha 6, 115-133
- Mosely, M.E.
- Pechey, J. 1694 The Compleat Herbal of Physical Plants. London
- Payne, E.J. 1892 History of the New World called America. New York

- Plowman, T. 1967 Folk uses of the New World
Aroids. Economic Botany 23(2).
104
- Prior, J. 1985 Structural changes on charring
Alwin, K.L. woods of Dichrostachys and Salix
from Southern Africa. Iawa
Bulletin. 4(4)
- Purseglove, J.W. 1968 Tropical Crops Vols. 1 and 2
Longman
- Redwood, Prf. 1885 The British Pharmacopoeia.
London Spottiswoode and Co.
- Reed, T. 1910 On the anatomy of some tubers.
Ann. of Bot. 24
- Renvoize, B.S. 1970 Manioc (Manihot esculenta
Crantz) and its role in the
Amerindian agriculture of
tropical America. Unpub. M. Phil
thesis Univ. London

- Richards, J.C. The Stonehenge Environs Project.
English Heritage Archaeological
Report Forthcoming
- Rindos, D. 1980 Symbiosis, instability and the
origins and spread of
agriculture: A new model. Current
Anthropology 21, 751-772
- Rindos, D. 1984 The origins of Agriculture - An
evolutionary perspective. New
York Academic Press
- Rogers, D.J. 1980 Edible, medicinal, useful and
poisonous wild plants of the
Northern Great Plains - South
Dakota Region. Sioux falls:
Biology Dept., Augustura College
- Rosendahl, P. 1971 Fossil sweet potato remains from
Yen, D.E. Hawaii. J. Polynesian Soc. 80,
379-385
- Rymer, L. 1976 The history and ethnobotany of
bracken. Bot. J. Linn. Soc. 73,
151-176

- Sablon, L.Du. 1902 Sur le tubercule du Tamus
communis. Rev. Gen. de Bot. 14,
145
- Sauer, C.O. 1952 Agricultural origins and
dispersal. New York
- Sauer, C.O. 1959 Age and area of American
cultivated plants. Actas 33rd
Internationales Congress
Americanistes VI 215-229
- Schery, R.W. 1954 Plants for man. London Allen and
Unwin
- Sharman, B.C. 1939 The development of the sucker of
Orchis mascula. J. Linn. Soc. Bot.
52, 145-158

- Specht, R.C. 1958 An introduction to the
ethnobotany of Arnhem land. In:
C.P. Mountford (ed.) Records of
the American Australian
expedition to Arnhem land, III.
Botany and Plant ecology, 479-503
M. Univ. Press
- Sifton, H.B. 1945 Air spaces tissue in plants. Bot.
Rev. 11, 108-143
- Sifton, H.B. 1957 Air space tissue in plants II.
Bot.Rev. 23, 303-312
- Simmons, I.G. 1979 Biogeography: Natural and
cultural. London Edward Arnold
- Small, E. 1978 A numerical taxonomic analysis of
the Daucus carota complex. Canad.
J. Bot. 56, 248-276
- Smith, C.E. 1980 Plant remains from Guitarrero
cave. In: T.F. Lynch (ed.)
Guitarrero Cave - Early man in
the Andes. 87-120 New York
Academic Press

- Specht, R.C. 1958 An introduction to the
ethnobotany of Arnhem land. In:
C.P. Mountford (ed.) Records of
the American Australian
expedition to Arnhem land, III.
Botany and Plant ecology, 479-503
M. Univ. Press
- Sifton, H.B. 1945 Air spaces tissue in plants. Bot.
Rev. 11, 108-143
- Sifton, H.B. 1957 Air space tissue in plants II.
Bot.Rev. 23, 303-312
- Simmons, I.G. 1979 Biogeography: Natural and
cultural. London Edward Arnold
- Small, E. 1978 A numerical taxonomic analysis of
the Daucus carota complex. Canad.
J. Bot. 56, 248-276
- Smith, C.E. 1980 Plant remains from Guitarrero
cave. In: T.F. Lynch (ed.)
Guitarrero Cave - Early man in
the Andes. 87-120 New York
Academic Press

- Smith, H.H. 1923 Ethnobotany of the Menomini
Indians. Bull. of the Public
Museum of the City of Milwaukee
4(1), 1-175
- Smith, H.H. 1923 Ethnobotany of the Ojibwe
Indians. Bull of the Public
Museum of the City of Milwaukee
4(3), 327-532
- Smith, J. 1882 A dictionary of the popular names
of the plants which furnish the
Nalevel and Aquered wants of man,
in all matters of domestic and
general economy, their history
products and uses. London
- Smith, P.M. 1976 Parsnips. In Evolution of Crop
Plants. N.W. Simmonds. (ed.).
323 Longman. London
- Snaydon, R.W. 1973 Ecological factors, genetic
variation and speciation in
plants. In: V.H. Heywood (ed.)
Taxonomy and Ecology London/New
York Academic Press

- Snaydon, R.W. 1984 Intraspecific variation and its taxonomic implications. In: Heywood and Moore (eds.) Current concepts in plant taxonomy ch II Academic Press
- Standifer, M.S. 1987 The identification of vegetative plant parts. Paper of Annual Conference of the Society of Ethnobotany, Gainesville, Florida
- Stant, M.Y. 1964 Anatomy of the Alismataceae. J. Linn. Soc. Bot. 59, 1-42
- Stant, M.Y. 1967 Anatomy of the Butomaceae. J. Linn. Soc. Bot. 60, 31-60
- Stebbins, G.L. 1974 Flowering plants - Evolution above the species level. Harvard University Press
- Stoller, E.W. 1972 Yellow nut sedge tuber
Nema, D.P. germination and seedling
Bhan, V.M. development. Weed Sci. 20(1)
93-97

Tackholm, V. Drar, M.	1950	<u>Flora of Egypt</u> Vol. II Fovard University Press Cairo
Tanaka, T.	1976	<u>Tanaka's cyclopedia of edible plants of the world.</u> Keigaku Publishing Co. Tokyo Japan
Theophrastus	1644	<u>De Historia Plantarum Libri decem.</u> Amsterdam
Thompson, D'A,	1917	<u>On growth and form.</u> Cambridge
Thompson, R.C.	1949	<u>A dictionary of Assyrian botany.</u> The British Academy
Tomlinson, P.B.	1969	<u>Anatomy of the Monocotyledons III: Cammelinales - Zingiberales.</u> Oxford University Press
Tootill, E.	1984	<u>The Penguin dictionary of botany.</u> Penguin Books
Towle, M.	1961	<u>The ethnobotany of pre-Columbian Peru.</u> New York

- Travis, H.P. 1973 The terms - rhizome and stolon.
Plant life 29, 46-47
- Turesson, G. 1922 The species and variety as
ecological units. Hereditas 3,
100-113
- Turesson, G. 1922 The genotypical response of the
plant species to the habitat.
Hereditas 3, 211-350
- Turesson, G. 1925 The plant species in relation to
habitat and climate. Hereditas 6,
147-236
- Turner, N.J. 1981 A gift from the raking: The
untapped potential of some food
plants of North American native
peoples. Canad. J. Bot. 59, 2231-
2357

- Turner, N.J. 1982 Two important 'root' foods of the
Kuhnlein, H.V. Northwest coast Indians: Spring
Bank Clover (Trifolium
wormskioldii) and Pacific
Silverweed (Potentilla anserina
ssp. pacifica). Economic Botany
36(4). 411-432
- Ugent, D. 1981 Prehistoric remains of the sweet
Pozorske, S. potato from the Casma Valley of
Pozorske, T. Peru. Phytologica 49(5), 401-415
- Ugent, D. 1982 Archaeological potato tuber
Pozorske, S. remains from the Casma Valley of
Pozorske, T. Peru. Economic Botany 36, 182-192
- Ugent, D. 1984 New evidence for ancient
Pozorske, S. cultivation of Canna edulis in
Pozorske, T. Peru. Economic Botany 38(4), 417-
432
- Ugent, D. 1986 Archaeological manioc (Manihot)
Pozorske, S. from coastal Peru. Economic
Pozorske, T. Botany 40(1), 78-102

- Ugent, D. 1987 Potato remains from a late
Dillehay, T. Pleistocene settlement in south
Ramirez, C. central Chile. Economic Botany
41(1), 17-27
- Unger, F. 1859 U.S. Pat. Off. Rpt. 308
- Uphof, J.C.Th. 1968 Dictionary of economic plants.
Verlag von J. Cramer
- Vavilov, N.I. 1926 Studies on the origin of
cultivated plants. Leningrad
- Waddington, C.H. 1957 The strategy of genes. London
Allen and Unwin
- Warning W.C. 1934 Anatomy of the vegetative organs
of the parsnip. Bot. Gaz. 96, 44-
72
- Watt, A.S. 1979 A note on the aeration and
aerenchyma in the rhizome of
bracken (Pteridium aquilinum (L.)
Kuhn. var aquilinum) New Phytol.
82, 769-776
- Werth, E. 1937 Abstammung und heimat des
Rettiche. Argew. Bot. 19, 194-205

- Wilder, G.J. 1974 Symmetry and development of
 Butomus umbellatus (Butomaceae).
 Am. J. Bot. 61, 378-394
- Wilson, D.G. 1983 The carbonisation of weed seeds
 and their representation in
 macrofossil assemblages. In: 6th
 Symposium Palaeoethnobotany /
 Groningen
- Wing, E.S. 1979 Palaeonutrition - Method and
Brown, A.B. theory in Prehistoric foodways.
 London Academic Press
- Winton, A.L. 1935 The structure and composition of
Winton, K.B. foods. Vol. II
- Wren, R.C. 1950 Potters cyclopaedia of botanical
 drugs and preparations. Potter
 and Clarke London
- Youngken, H.W. 1919 Notes on the dahseen and chayobe.
 Am. J. Bot. 6, 380-386
- Zohary, D. 1988 Domestication of plants in the
Hopf, M. Old World. Oxford University
 Press